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LATE CAMBRIAN AND EARLY ORDOVICIAN TRILOBITES FROM THE MARATHON UPLIFT, TEXAS[1]

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ABSTRACT—Trilobite faunas in the Marathon folded belt of West Texas (1) from the Upper Cambrian-Lower Ordovician beds of the Dagger Flat and Marathon formations and (2) from exotic boulders of the same age near the top of the Middle Ordovician Woods Hollow shale are of particular interest because many genera belong to the Atlantic province rather than to the nearby North American faunal realm. Probably the Late Cambrian and Tremadocian olenid faunas of South America were distributed northward through the Andean and Ouachita troughs and east and southeastward around an outer Appalachian trough to Acadia and Europe following a facies belt of argillites and dark limestones.

The exotic boulders show in part a mixture of trilobite genera of both Atlantic and North American provinces in a less terrigenous lithofacies than that of the shale and flaggy limestone of the Cambro-Ordovician sequence found in place.

They are probably erosional remnants from an Ordovician uplift toward the foreland side of the trough and present problems similar to those of the Rysedorph and Lévis conglomerates. Some of the Late Cambrian boulder faunas are older than any known from the in situ formations of the Marathon folds.

The mixed faunas in the boulders enable more detailed correlation between the two provinces. The American *Cedaria* zone is probably older than any olenid fauna in this area. *Parabolinella evansi* and other olenids are associated with a high *Aphelaspis* fauna. Tremadocian genera from the boulders indicate contemporaneity with the Dagger Flat and lowest Marathon formations based on associations in Europe and South America; genera in the same rocks show equivalence to the American Gasconade and possibly also Roubidoux.

A new crepicephalid genus, *Nasocephalus*, is described with *N. nasutus*, n. sp., as type species. Other new species described are *Nasocephalus flabellatus*, *Coosia pernamagna*, *Bemaspis dubita*, *Wilbernia ? minuta*, and *Beltella latifrons*. Some of the American olenids are described in more detail than previously. Many fragmentary specimens remain only tentatively identified.

ADDENDUM

ON THE correlation chart in this paper equating Atlantic province zones with those of the North American Late Cambrian, the *Cedaria* zone of the latter area is considered unrepresented in the Scandinavian sequence, and the uppermost *Paradoxides* fauna equivalent to the American *Bolaspidella* (latest Middle Cambrian) fauna. While this paper was in press Dr. A. H. Westergård of Sweden published descriptions and illustrations of *Agraulos difformis* and *A. anceps* from the zone of *Solenopleura brachymetopa* immediately un-

[1] Published with authorization of the Director, Bureau of Economic Geology, The University of Texas.

derlying the zone of *Lejopyge laevigata* in the Bornholm and Andrarum sections. Two species, *Nasocephalus nasutus* and *N. flabellatus*, described in the writer's paper are very close to the Swedish species, almost certainly congeneric with them. These are found in the *Cedaria* zone boulders of the Woods Hollow shale, emphasizing again the Atlantic Province aspect of the boulder faunas. It is thus possible that beds in Sweden with *Paradoxides forchhammeri* and *Centropleura loveni* (occurring with *Solenopleura brachymetopa*) are as young as the American *Cedaria* zone.

Dr. Westergård's recent paper[2] describes also species of the genus *Grönwallia* from this same zone. Both pygidium and cranidium of this form resemble those of the American index genus *Aphelaspis*, as do species of *Nericia* from the overlying zone of *Lejopyge laevigata* (Westergård, 1948). These are probably progenitors of the American genus which makes its first appearance in the Marathon area somewhat later in Woods Hollow boulders with olenid faunas.

INTRODUCTION

Investigations for the Bureau of Economic Geology, The University of Texas, in the summers of 1951 and 1952 have resulted in collections of Late Cambrian and Early Ordovician exotic boulders found in the Middle Ordovician Woods Hollow shale of the Marathon uplift in West Texas. The writer is indebted to the Bureau of Economic Geology for sponsoring the project and to Drs. John T. Lonsdale and Virgil E. Barnes for help and encouragement in the study of the trilobites found in these boulders and in the Dagger Flat and Marathon beds of the Marathon region. The writer is especially grateful to Dr. Christina Lochman Balk for her criticism both of text and organization of the paper. Drs. Rousseau Flower and Harry B. Whittington have aided in identifying some of the Lower Ordovician fossils.

Approximately 100 boulders have been collected from six localities, and although many are unfossiliferous, a total of several hundred fragmentary specimens permits recognition of five trilobite faunas from them. All collections and types are with The University of Texas Bureau of Economic Geology.

At the beginning of work a correlation of the exotic boulder faunas with those of the sparsely fossiliferous lower Marathon and underlying Dagger Flat formations became of interest. These beds occur lower in the stratigraphic sequence than the boulder-bearing Woods Hollow shale; their limited and very poorly known fossils indicated possible contemporaneity with the strata represented by the boulders. Consequently, an attempt was made to collect enough trilobite specimens to learn the precise age of these Cambro-Ordovician beds lying in place. The study shows that the lower part of the Marathon formation contains almost completely Atlantic province genera of Tremadocian age. The upper beds of the underlying Dagger Flat formation may also be Tremadocian.

The oldest trilobites identified from it are probably high in the Atlantic province Upper Cambrian. The faunas from the Woods Hollow boulders are mainly of older Upper Cambrian than the English Tremadoc. Both Atlantic province and North American types of trilobites are represented in different boulders, but some boulders contain genera found in both faunal realms which are useful in effecting better interprovince correlation.

The beds whose faunas are described in this paper are not very fossiliferous and in most places the material described is scanty and incomplete. For this reason identifications are questioned in many places and merely a comparison with some better-known species is indicated in some instances. Much more study of the fossils is possible for extremely prolific faunas of agnostids and acrotretoid brachiopods were broken out or etched from the matrix with acetic acid. Further search of the lower Marathon beds should result in important collections of other Atlantic province trilobites, and an exact correlation between the graptolite zones of the shale sequences and those of the typically carbonate Canadian sequence could probably be made.

STRATIGRAPHY OF THE DAGGER FLAT AND LOWER MARATHON FORMATIONS

Early Ordovician deposits of the Southwest appear to occur in three lithofacies re-

[2] Westergård, 1953.

flecting (1) a wide shallow warm-water shelf area (the Ellenburger dolomite sequence with a gastropod and nautiloid fauna), (2) a cooler, perhaps deeper, and more turbid-water environment (with a brachiopod fauna) occupying more negative areas and exposed as the El Paso and Arbuckle limestones, and (3) the predominantly fine clastics (graptolite shales) of the Ouachita-Marathon belt deposited south and east of the shelf area (Cloud and Barnes, 1948, pp. 63–65; King, 1937, pp. 42–47). The latter beds are at present in close proximity to the shelf deposits because of Pennsylvanian thrusting. It is difficult if not impossible to conceive of them as normal geosynclinal deposits because they are somewhat thinner than the dolomite and limestone facies of the continental interior, but they differ greatly lithologically and faunally from the shelf sediments and occur in a linear and arcuate trend along the site of the Late Paleozoic Ouachita geosyncline. The Marathon Lower Ordovician sequence is more calcareous than its counterpart in the Ouachitas and seems transitional between the Arbuckle type of limestone and the shales and sandstones of the Collier, Crystal Mountain, and Mazarn formations of southeastern Oklahoma. Figure 1 is a preliminary lithofacies and paleogeographic map illustrating the geographic distribution of the facies during early Ordovician times.

The Dagger Flat and Marathon formations are of great interest because they bear Atlantic province faunas in an isolated location approximately halfway between the better known but widely separated deposits of Acadia and the Paleozoic Andean trough of Argentina, Bolivia, and Colombia. Biostratigraphic studies of the Marathon formation are very incomplete, but most of the Dagger Flat outcrops mapped by King have been re-examined for fossils and in those with simple enough structure, sections have been measured. The Dagger Flat crops out only along the two main anticlinal axes of the Marathon folded belt (fig. 2).

As King previously indicated (1937, p. 22), the Dagger Flat may be divided into two units. The lower is represented by the oldest beds exposed in Dagger Flat along the anticlinorium of that name approximately 1.5 miles southeast of Buttrill's ranch house and is typically a graywacke sandstone and shale sequence with but a few thin sandy chocolate-weathering limestone flags. In the writer's experience it is completely unfossiliferous and together with the upper shaly member is much thicker than King estimated. The writer here names the lower unit the Buttrill Ranch member.

I propose the name Roberts Ranch member for the rock types occurring in the higher beds of the Dagger Flat formation from the outcrops along the crest of the Marathon anticlinorium which is traversed by Roberts ranch road south of the Alsate Creek graptolite locality (King, 1937, p. 28, fig. 12). The member is principally shale but possesses thin beds of dark sandy finely crystalline limestone and calcareous micaceous graywacke sandstone. These have been described in some detail by King (1937, p. 22). The Roberts Ranch member has been designated in both of its outcrop belts as lying below prominent limestone pebble conglomerates interbedded with dark shale. These beds are considered basal Marathon formation, although typical Marathon limestones (that is, dark finely crystalline, bluish-white weathering) first occur about a hundred feet stratigraphically above the conglomerates. In the exposures along Dagger Flat, the only place where the older member is exposed, the Roberts Ranch beds are more arenaceous and much less fossiliferous than at their type locality, but nevertheless lithologically distinct from the more massive sandstone beds of the Buttrill Ranch member.

Section in Dagger Flat

LOWER MARATHON FORMATION	*Feet*
Limestone, dark gray, slabby, weathering light bluish to medium bluish gray with thick interbeds of shale. Several ledges of flat limestone pebble conglomerate (1 to 3 ft. thick), light orange brown weathering, sandy limestone and pure aphanitic laminated limestone. More shale in lower half.	195
Shale, moderate yellowish brown, calcareous, with *Bryograptus* (100 yards NE of stone cairn) (Base of above interval)	
Shale and slabby limestone as described above	55
Conglomerate, flat limestone pebble, shale and limestone flags. Lowest conglomerate bed is base of interval	90
Total	340

DAGGER FLAT FORMATION

ROBERTS RANCH MEMBER

Limestone, shale, and sandstone, thin-bedded	300
Mostly covered, fossiliferous limestone at base with inarticulate brachiopods	110
Shale and thin beds of sandstone, mostly covered; some limestone flags. Pebble conglomerate at base	85
Covered; top third of interval separated from rest by fence	75
Total	570

BUTTRILL RANCH MEMBER (type locality)

Massive rounded-weathering coarse graywacke sandstone and some fine sandy conglomerates	50
Shale with many thin-bedded, finely cross-bedded calcareous sandstone flags	320
Total	370

(axis of isoclinal fold lies NW of this interval)

SECTION 4 MILES SW OF MARATHON

LOWER MARATHON FORMATION	Feet
Lowest pure limestone in section: dark gray, aphanitic, nodular, thin-bedded, weathers chalk-white	10
Shale, mostly covered	80
Limestone (1 to 5 ft. beds) dark gray, weathering light bluish to medium bluish gray alternating with conglomerate, flat limestone pebble type and 20 to 80 ft. beds of shale. Coll. 7 at base. *Schizograptus* and *Bryograptus*	120
Shale, thick beds alternating with 1 ft. beds of flat limestone pebble conglomerate. Coll. 6, *Bryograptus*	75
Shale and flat limestone pebble conglomerate	5
Shale with dark yellowish brown flat limestone pebble conglomerate at base (1 ft. bed)	25
Limestone, dark gray, crystalline, pebbly, coll. 3 and 4 (3 ft. apart) with *Asaphellus, Symphysurina* cf. *S. woosteri, Beltella latifrons, Tostonia, Ophileta, Finkelnburgia*	8
Shale, greenish gray, lenses of coarse-medium grained brown sandy limestone and flat pebble conglomerate	30
Shale with some flaggy sandy dark gray limestone (fence line crosses section line)	70
Limestone, dark gray, slabby, coll. 2 with *Andesaspis argentinensis*	3
Shale and limestone flags, weathering dark yellowish brown	85
Conglomerate, coarse, flat limestone pebbles in beds 1 to 3 ft. thick interbedded with much dark gray shale	75
Total	486

DAGGER FLAT FORMATION

ROBERTS RANCH MEMBER

Shale, greenish gray, mostly covered	50
Limestone, sandy, fine-grained, finely cross-bedded, flaggy, dark gray; weathers moderate yellowish brown and interbedded with much greenish gray shale. Lower 10 feet forms ridge traceable for several hundred yards. Coll. 1 in base of these beds: *Leptoplastus* sp., *Geragnostus rudis, G. rudis* var. *holmi, Litagnostus*	175
Total	225

(axis of fold; section is duplicated beyond this point)

The Dagger Flat type section was measured perpendicular to the strike about ¾ mile northeast from the windmill and line house on Buttrill's ranch along a line trending N55°W from a large stone cairn. A dip of 70°SE is assumed for the beds in this line. Constant check of cross-bedding indicates that the isoclinal strata are not overturned and repeated. The Roberts Ranch member is best exposed in the above section measured 4 miles southwest of Marathon (abbreviated in the paleontological part of the present paper: 4 mi. SW Marathon). It is situated along the axis of the Marathon anticlinorium about 15 miles northwest of the type section in Dagger Flat and about 3 miles northeast from the exposures along Roberts ranch road. This section is reached by taking a road due west of Marathon for 2.4 miles to the site of Old Dragoo ranch (double windmills) and following a ranch trail south 1.5 miles. The outcrop lies northwest of a low ridge formed by the Monument Springs member of the Marathon formation and west of a north-trending fence line. This is the only continuous measured section which has enough fossils to give an idea of faunal sequence.

Other localities with fossils occur farther southwest along the southeast flank of the Marathon fold. It is not clear whether these fossils come from rocks properly placed in the Dagger Flat or Marathon formation. They are all from the outcrops mapped as Dagger Flat formation by King but probably occur in or above the main beds of limestone pebble conglomerate and are of Tremadocian age. The localities are designated by mileage along the Roberts ranch road (abbreviated: RR rd.) south from where it passes the Alsate Creek graptolite locality and turns south.

FIG. 1—Conjectured facies relations of Cambro-Ordovician time in West Texas. The position of the dark shale and thin limestone facies has been shifted by late Paleozoic orogeny. The distribution of the brown and gray limestone-dolomite facies is largely conjecture except in the Marathon Uplift.

RR rd. 1.1 mi.: In rise just above drain 200 yards west of road. Coll. A, *Geragnostus rudis, Bellefontia* sp., *Bellefontia* ? cf. *B. ? acuminiferentis* Ross, forked asaphid hypostome. Coll. B, asaphid pygidium undet., *Asaphellus* sp. undet., *Trigonocerca* pygidium.

RR rd. 1.5 mi.: Bed east of road composed of sandy limestone with numerous brown chitinous scabbards, conchostracans, *Shumardia* sp. undet. Overlain by yellow-weathering siliceous shale containing multiramous dichograptids.

RR rd. 2.8 mi.: Section measured on east side of gap between ridges of Marathon formation about ¼ mile south of point where road leaves small valley and crosses Marathon formation. Cannot be accurately correlated with the section 4 miles southwest of Marathon on lithic basis but is probably equivalent to the middle part of it.

MARATHON FORMATION	*Feet*
Limestone, pure, dark gray, massive, light bluish to medium bluish gray weathering, with typically Lower Ordovician nautiloid and gastropod.	
Shale, greenish black, base with *Clonograptus*	20
Shale, greenish black and limestone, sandy, dusky brown weathering. (Coll. 2, no fossils)	37
Conglomerate, flat limestone pebble	1
Shale, with few 3 to 4 inch beds of dusky brown fine-grained dark gray limestone. Unidentified trilobite related to *Elyx*	13
Shale, greenish gray interbedded with fine-grained limestone, sandstone, and abundant flat limestone pebble conglomerate	270
DAGGER FLAT FORMATION (top?)	
Shale, greenish gray and fine to medium-grained sandstone. Middle of interval contains coll. 1, brown chitinous scabbard-shaped fossils	50
Total	391

Faunas of the Dagger Flat and Marathon formations.—The lowest beds in the Dagger Flat formation containing identifiable trilobite remains occur at the base of the section 4 miles southwest of Marathon approximately 225 feet below the beds of coarse limestone pebble conglomerate marking the base of the Marathon formation in this section. They consist of the typical Swedish agnostids *Geragnostus rudis* and *G. rudis* var. *holmi* (Westergård, 1922, pl. 1, figs. 13–17) and fragments of cranidia and free cheeks belonging to the abruptae section of the olenids, probably the genus *Leptoplastus* since a tiny spinose pygidium common in this genus is associated with the fragments (Westergård, 1922, pl. 8, figs. 27, 29). These strata must correlate with Westergård's zones 4 or 5 (1947, p. 25); *Leptoplastus* is reported only from zone 4 but the agnostids occur in zone 5. The writer's material is too poor to preclude the identification of *Ctenopyge* instead of *Leptoplastus*, and a completely definite assignment is not considered possible at this time. Beds in the lower Marathon and also in the uppermost Dagger Flat as mapped by King along Roberts ranch road have yielded the typical middle and upper Tremadocian genera *Asaphellus, Shumardia, Beltella,* and *Andesaspis* associated with trilobites characteristic of North American limestone sequences, that is, *Symphysurina* and asaphids such as *Bellefontia.*

Other beds in the lower Marathon and highest Dagger Flat contain the graptolite genera *Bryograptus, Schizograptus,* and *Clonograptus* of the lower Deepkill and Lévis shales. *Dictyonema flabelliforme* has not been found by the writer in these lowest Ordovician beds but King reports it low in the Marathon. The writer has collected *D. flabelliforme* much higher in the Marathon formation (bed 7 of Bridge and Dake's Alsate Creek section; King, 1937, p. 29) immediately above the Monument Springs member with such Skiddavian forms as *Tetragraptus* cf. *T. fruticosus, Didymograptus extensus, Phyllograptus* sp., and the trilobites *Pliomerops* (?) and *Selenecem* (*Alsataspis* of authors).

THE WOODS HOLLOW BOULDERS

The Lower Ordovician formations, the Marathon limestone and Alsate shale, are overlain disconformably in the Marathon folded belt by the Fort Peña formation consisting of about 200 feet of sandy conglomeratic limestones and beds of characteristic purplish-weathering chert. These beds are overlain by a shale unit termed the Woods Hollow (400 feet thick) which is generally dark greenish clay shale with some thin layers of fine-grained dirty calcareous sandstone, slabby sandy limestone, and highly

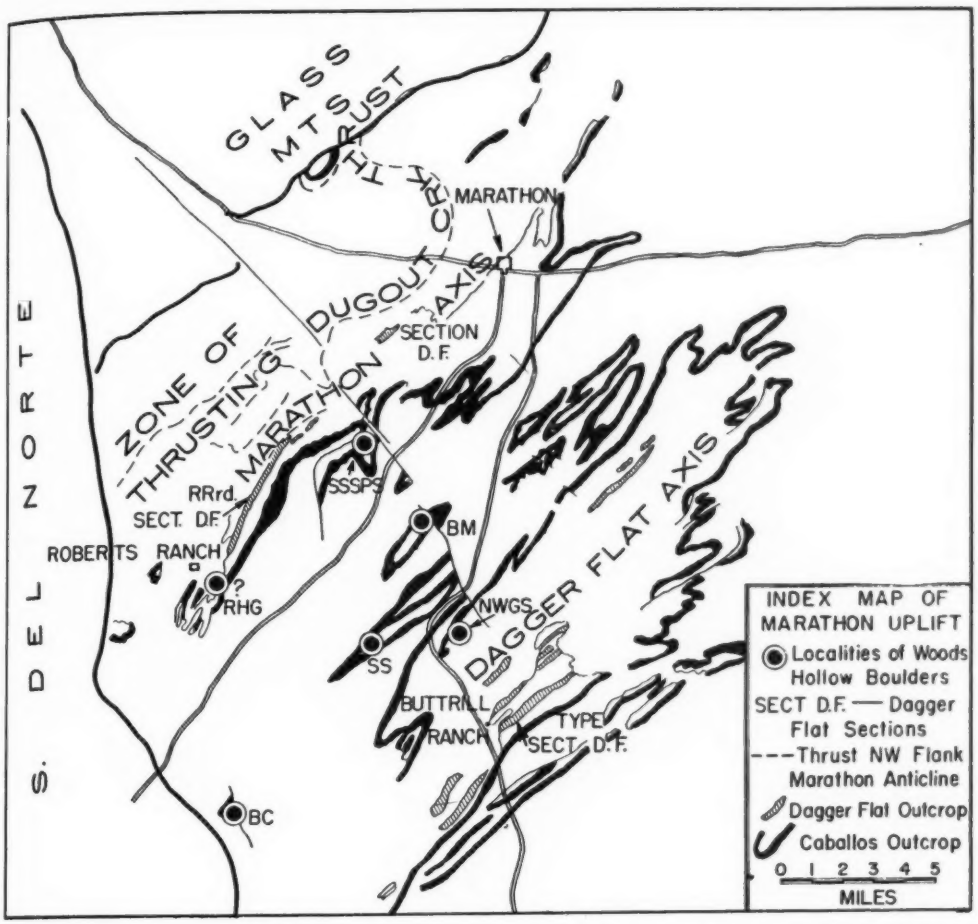


FIG. 2—Locality map of Marathon folded area showing distribution of Woods Hollow boulders and outcrops of Dagger Flat formation.

characteristic granular yellow-weathering limestone conglomerate. Both the Fort Peña and Woods Hollow formations contain Middle Ordovician graptolites: *Diplograptus* and *Climacograptus*. They are the clastic belt equivalents of the Simpson group of west Texas and Oklahoma; they occupy the same stratigraphic position and contain the same fauna as the Womble shale and sandstone of the Ouachita trough (King, 1937, p. 43).

At a few localities in the southwestern part of the Marathon basin the upper beds of the Woods Hollow shale contain scattered rounded limestone boulders of Early Ordovician and Late Cambrian age. The Woods Hollow is overlain disconformably by the Maravillas formation, several hundred feet of interbedded chert and dark clastic siliceous limestone. In the same general area in which the exotic boulders occur in the Woods Hollow shale, the basal Maravillas contains thick, very coarse conglomerate beds (King, 1937, p. 38).

The boulders, when first discovered by Baker and Bowman (1917, p. 83), were considered fossiliferous nodules in supposed Late Cambrian and "Ozarkian" argillaceous sequences underlying unconformably the Upper Ordovician Maravillas chert of the Marathon folds. These beds were named the "Brewster formation" and "member 1 of

the Marathon series." King (1937, pp. 24, 25) first recognized the boulders as exotics in the Woods Hollow shale, and the "Brewster formation" has been abandoned. Ulrich (in King, 1937, pp. 24, 25) identified faunas from the boulders and established their approximate age but failed to recognize any genera belonging to the Atlantic province.

Geographic distribution.—The original Woods Hollow boulder localities of Baker and Bowman are (1) 1 mile north of the south end of Simpson Springs Mountain (SS-#) and (2) at the north end of East Bourland Mountain (BM-#). In both localities the boulders occur at the heads of deep shale valleys and structurally along plunging anticlinal axes in much contorted shale. King examined and photographed these locations (1937, pl. 5E, 6B) and discovered another locality (3) northwest of Garden Springs about 1 mile (NWGS-#). The writer after considerable search located others: (4) just west of the Big Bend Park highway 1 mile west of Garden Springs (poor); (5) along the Sunshine Springs overthrust just southwest of Roberts ranch road (SSSPS-#, poor); (6) 1 mile north of Rock House Gap (questionable); and (7) 1 mile north of Stuart's place on southwest side of Bear Canyon (BC-#). The localities are all situated toward the southwest side of the Marathon uplift and west of the zone of pronounced tear-faulting which truncates the north end of East Bourland Mountain, passes north of Sunshine Springs Mountain and south of "The Post" (picnic grounds, near Fort Peña, Colorada; see fig. 2). Woods Hollow outcrops southeast of the known localities and northeast of the tear-fault zone have been searched in vain for the boulders. The boulders are more numerous and larger at Simpson Springs Mountain, but no great differences exist in the kinds of boulders at different localities. At least one kind (type 1, pink mottled massive limestone) is common to all places.

Types of boulders.—The exotics are composed exclusively of types of limestone; these are varied enough to represent possibly many different formations, but study of both faunas and rock types delineates clearly only seven possible stratigraphic units from which the boulders may have been derived. Listed in biostratigraphic order these are:

1. Pale brown to grayish orange pink aphanitic to fine-grained glauconitic mottled limestone. Very large boulders, most common and most widely distributed, occurring at all localities. The mottling is similar to that of Cambro-Ordovician algal bioherms. Interspersed in the rock occur numerous acrotretoid and oboloid brachiopods, pelmatozoan stems, and a single small gastropod. Age: either Late Cambrian or Canadian.
2. Dark gray, fine-grained dolomite or limestone. Small boulders abundant only at Simpson Springs Mountain. Contains abundant pelmatozoan stems. Age: either Late Cambrian or Canadian.
3. Brownish gray mottled with purplish tinge, fine-grained, slightly sandy limestone of fragmental texture, with glauconitic matrix and phenoclasts of pink fine-grained limestone; some calcirudite mixed with fine-grained limestone; weathers purplish and is highly jointed. At least five large blocks at Simpson Springs locality, one at Bourland Mountain, and one at Bear Canyon. Fossils scarce but varied, including conodonts, nautiloids, gastropods, and trilobites. Age: Gasconade (Tremadoc).
4. Moderate yellowish brown weathering medium-grained limestone. Two or three blocks from northwest of Garden Springs and one large block from Bear Canyon. Age: medial Late Cambrian (medial Franconian).
5. Very light gray pure medium-grained limestone coquina. A very few small boulders only at Simpson Springs and East Bourland Mountain with an olenid fauna. Age: probably *Olenus* zone (Westergård's zone 2 but possibly Franconian). See faunal discussion.
6. Dark gray to brownish black fine-grained limestone, slightly fossiliferous; containing lenses of pebble conglomerate with abundant fragments of agnostids, olenids, and *Aphelaspis* zone trilobites in both the matrix and in the pebbles. Few boulders confined to East Bourland Mountain. Most of the collection comes from one block approximately 2 feet in diameter (BM-4). Age: medial Late Cambrian (late Dresbachian).

7. Dark yellowish brown to moderate yellowish brown medium-grain mottled limestone, weathers with orange ferruginous spots and contains lenses of trilobite coquina. Blocks up to 1½ feet long and ½ foot thick. Contains an unusual early Dresbachian (*Cedaria* zone) fauna.

A review of the limestone types found in the boulders indicates that they are probably intermediate between the light-colored pure oölitic glauconitic and rather coarsely fragmental and highly fossiliferous Late Cambrian and Early Ordovician limestones of such platform areas as the Llano Uplift, and the argillaceous dark bituminous fine-grained limestone of the Ouachita-Marathon belt. The fossiliferous limestones of the boulders are predominantly gray, pink, or brown and are mainly bituminous and fine-grained, but evidently part of the original strata contained large lenses or layers of trilobite coquina and intraformational conglomerate since some of the larger boulders consist solely of this material.

Physical appearance and relation to matrix.—The boulders are actually well-rounded slabs being longer and wider than thick and having a characteristic nodular weathered surface. They are of many sizes and vary from a few inches in greatest diameter to several feet across. Probably they average less than 1 foot in largest dimension with the other dimensions half or two-thirds the greatest and are roughly rectangular in shape. One block (type 1) is about 10 feet long and at least 3½ feet thick. The bedding and jointing of the limestone controlled the shape and size of the boulders; their long dimension is parallel to the bedding plane of the rock. It is difficult to ascertain whether the weathered periphery of the boulders may be attributed to recent weathering or to decomposition during transport in Ordovician times. Almost all of the boulders occur in weathered shales or have fallen out of the matrix and lie as litter on a talus slope.

The boulders come from rock having suffered little or no structural deformation. The fossils are undistorted and, except for strongly developed jointing in the Lower Ordovician boulders of type 3, there is no sign that the original rock formations were more than gently folded or faulted.

No definite observation was possible on the relation of boulder clusters to bedding. At least some boulders at Simpson Springs Mountain may have been strewn out on a bedding plane, yet most of the boulders are weathered from the shale and at places where they can still be observed in place, the incompetent shale has wrapped around the limestone blocks due to Pennsylvanian folding. Indeed, immediate distinction between limestone nodules of the upper Woods Hollow shale and the exotic blocks is difficult in some places.

The boulders occur generally toward the top of the Woods Hollow (15 to 55 feet beneath the overlying Maravillas formation) but some have been found in doubtful structural position well down in the formation.

The writer considers the following facts relative to the origin of the boulders to be established:

1. They were derived from medium to thick-bedded predominantly limestone strata probably many hundreds of feet thick and representing most of Late Cambrian time and at least very early Canadian time.
2. The present very restricted distribution of the boulder localities on the southwestern side of the Marathon basin indicates a rather local source area to the west or northwest of the clastic trough area in which the Woods Hollow shales were deposited. (Thorough search of the Woods Hollow beds both northeastward and southeastward in the Marathon belt as well as in the Solitario Uplift has failed to produce any boulders.)
3. Both faunally and lithologically the boulders are more related to the strata on the shelf or foreland side of the Marathon belt than to equivalent strata in the Marathon folded belt (see faunal discussion).
4. The region from which the boulders were derived was probably an up-faulted block or only moderately folded belt with undistorted rocks.
5. Transportation and weathering by water is involved at some point in the history

of the boulders. The nodular weathered surface and degree of rounding could have been caused by either stream transport or wave action. Large size of some of the water-rounded boulders suggests a very short distance of transport.

6. The patchy distribution of the boulders, their great irregularity in size, and their location in a thick body of marine shale preclude an origin as an ordinary marine conglomerate.

Origin and geological history of the boulders.—The above facts point toward an explanation of the origin of the boulders given by King (1937, p. 47) who considered that they were derived from an uplift on the foreland side of the Marathon belt of clastic sedimentation. Exactly how they were emplaced in the shale is yet unanswered. Further study of the boulders and comparison with other Ordovician exotics (Rysedorph Hill, Lévis, and Cowshead conglomerates) is requisite to a final explanation of these unusual deposits. Present evidence suggests to the writer that the Woods Hollow blocks slumped off a Middle Ordovician fault scarp (probably represented by a series of sea cliffs paralleling the western and northern edges of the Marathon depositional belt). They may have been rounded at water's edge by wave action and later emplaced in the graptolite-bearing silty muds of the Woods Hollow formation by violent storms or turbidity currents. It is possible that the smaller blocks might have been stream-transported for some distance from a wide-spread rather than local source area, but most of the boulder types are represented by at least one block one or two feet in diameter indicating a near-by point of origin.

The uplift which furnished the limestone boulders may have been planed down and overridden in Pennsylvanian times by the folds and thrusts now seen in the Marathon Uplift. This is inferred because the closest Canadian strata to the Marathon belt known in such wells as the Welch Espy, northwest Presidio County, and the Hinton Dodson, Texas American Syndicate on Hovey dome, Brewster County, are light-colored dolomite (with some limestone) of typical Ellenburger facies. These beds are underlain by a relatively thin section of sandstone of either earliest Ordovician or latest Cambrian age. The section in these wells thus differs considerably from the dark glauconitic limestone of the Woods Hollow boulders which show an extensive Late Cambrian as well as Early Ordovician section and from the contemporaneous argillaceous beds of the Marathon and Dagger Flat formations.

The Welch Espy well lies 50 to 60 miles from the postulated Marathon front of folding (exposed closest in the Solitario Uplift), but the Hovey dome well lies only 30 miles from the nearest exposures of the Marathon formation. Here at least exists a juxtaposition of the Ellenburger facies with the dark fine-grained argillaceous beds bearing typically Atlantic province trilobites. The Dagger Flat and Marathon formations have been thrust northwestward (King, 1937, pl. 15), narrowing to an unknown extent the belt of transitional facies. This facies is conjectured to be limestone of the type now preserved as remnants in the exotic boulders. The eastern edge of this facies is probably now overlain by the Marathon folds (see fig. 1).

Discussion of faunas and their interprovince correlations.—Faunas from the boulders are discussed in stratigraphic sequence. Certain faunas not found in the Marathon Uplift are discussed because of their bearing on world-wide correlations depicted in figure 3.

The oldest trilobite fauna from the Woods Hollow boulders belongs to the *Cedaria* zone (boulder type 7). Several faunules may be represented by the boulders, but enough specimens in common are found to consider the group of boulders as a faunal unit. The key species is *Cedaria* aff. *C. gaspensis* Rasetti. The species has been identified from only a few of the boulders but the genus is found in most of the boulders assigned to the zone. In most cases fragmentary material prohibits certain identification of the *Cedaria* species.

Rasetti's *Cedaria* species occurs in one of the boulders of the Lévis conglomerate found at Grosses-Roches and also in the Murphy Creek formation of extreme eastern Gaspé. A species of *Blountina* from Woods Hollow boulders SS-24 shows affinity with Rasetti's *Blountina westoni* which occurs in the same boulder at Grosses-Roches. The

TABLE 1.—FAUNAS FROM WOODS HOLLOW BOULDERS

Boulder type 3 Ordovician species:	SS-30		SS-36	SS-37	SS-38	BC-1
Sinuopea sp.	—	—	—	X	—	—
Rhombella umbilicata ?	X	—	—	—	—	—
Schizopea sp.	X	—	—	X?	—	—
Oistodus sp.	X	—	—	—	—	—
Baltoceratid nautiloid	X	—	—	—	—	X
Pseudohystricurus sp.	X?	—	—	X	X	—
Parahystricurus sp.	X	—	X	—	—	—
Apatokephalus serratus	—	—	X	—	—	—
Parabolinella triarthroides ?	—	—	X	—	—	—
Platycolpus cf. *P. capax*	—	—	—	—	X	—
Asaphid	—	—	—	—	X	—
Geragnostus sp.	X	—	—	—	—	—
Pseudagnostus sp.	—	—	—	—	X	—
Homagnostus sp.	—	—	—	X	—	—

Boulder type 4 Middle Franconian species		NWGS-6			BC-2	
Taenicephalus sp.	—	X	—	—	X	
Wilbernia sp.	—	—	—	—	X	
Wilbernia (?) *minuta*	—	X	—	—	X	
Bemaspis dubita	—	—	—	—	X	
Pseudagnostus josephus	—	—	—	—	X	

Boulder types 5 and 6	(type 5)				(type 6)	
Olenid-*Aphelaspis* species:	SS-26	SS-27	BM-new	BM-2	BM-4	BM-8
Parabolinella incerta	X	X	X	X	—	—
Olenus cf. *O. truncatus* (fragments only)	—	—	—	X	X	—
Parabolinella evansi	—	—	—	—	X	—
Olenid free cheek (continuae)	—	—	—	—	—	X
Pterocephalina cf. *P. grata*	—	—	—	X	X	—
"Taenicephalus" megalops Kobayashi	—	—	—	—	X	—
Aphelaspis sp. undet.	—	—	—	—	X	—
Aphelaspis cf. *A. walcotti*	—	—	—	—	X	X
Pseudagnostus josephus	—	—	—	X	—	—
Pseudagnostus ? sp.	X	X	—	—	—	—
Pseudagnostus cyclopyge	—	—	—	—	X	—
Homagnostus obesus	—	—	—	X	X	—
Glyptagnostus reticulatus (fragment only)	—	—	—	—	X	—

ubiquitous genus *Blountia* is abundantly represented by two species, *B. assimilis* Resser from the Nolichucky of the Appalachian trough and *B. ovata* Duncan originally described from the Pilgrim formation of the Little Belt Mountains, Montana. A new genus *Nasocephalus* is represented by two species, and both *Kormagnostus* and *Pseudagnostus* are extremely abundant. A great variety of agnostids exists in these boulders but are not described in this paper.

Little similarity exists between the *Cedaria* fauna from the boulders and that known from the lower Riley formation of the Llano Uplift (comparison made with aid of unpublished manuscript by A. R. Palmer). The *Cedaria* species of the Hickory sandstone are quite different from *C. gaspensis* and indeed even the generic makeup of the faunas is dissimilar. The relation of two species with Dresbachian forms from the Lévis boulders is noteworthy inas-

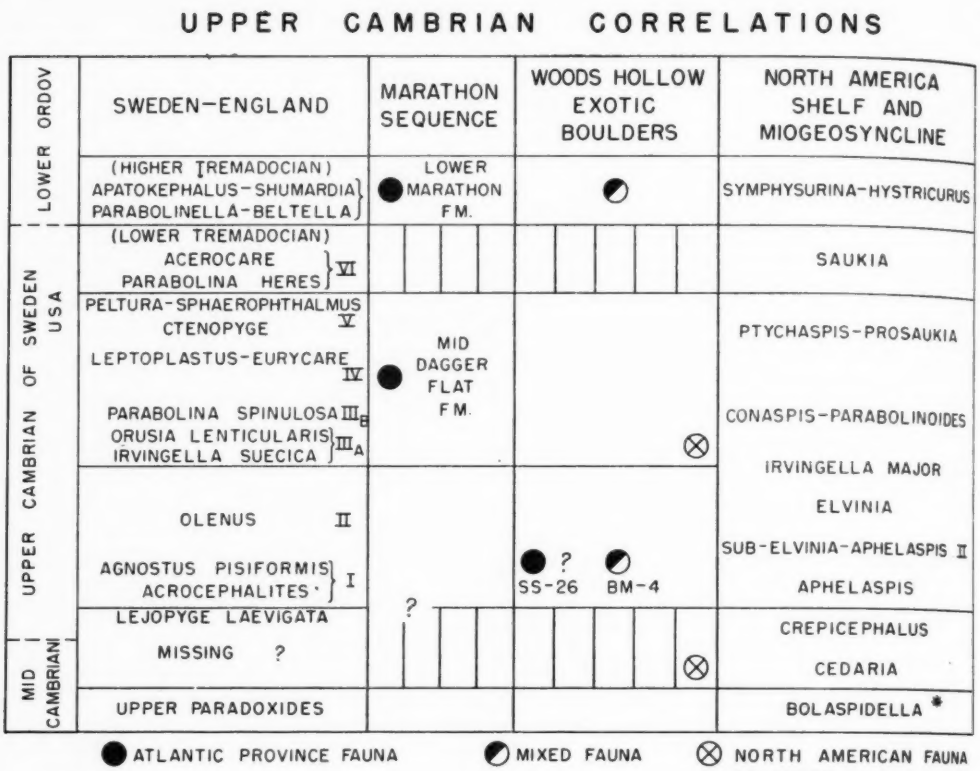


FIG. 3—Upper Cambrian correlations between Atlantic and North American faunal provinces with probable positions of faunas of in situ Cambro-Ordovician strata and the Woods Hollow boulders. Series of vertical lines indicate that no positive correlation is possible at these levels.

TABLE 2.—*Cedaria* ZONE SPECIES FROM WOODS HOLLOW BOULDERS

Boulder type 7	SS-24	SS-29	SS-31	SS-32	SS-33	SS-34	SS-35	BM2a	BM-3	BM-7
Cedaria aff. *C. gaspensis*	—	X	—	—	X	—	X	—	—	—
Cedaria sp.	X	—	—	X	—	X	—	—	X	X
Blountia assimilis	—	—	X	—	X	—	—	—	—	—
Blountia ovata	X	—	—	X	X	—	—	X	—	—
Blountiella sp.	—	—	—	X	—	—	—	—	—	—
Blountina aff. *B. westoni*	X	—	—	—	—	—	—	—	—	—
Coosella sp.	—	—	—	—	—	—	X	—	—	—
Coosia pernamagna	X	—	—	X	—	—	—	—	—	—
Nasocephalus nasutus	—	—	—	X	X	—	—	—	—	—
Nasocephalus flabellatus	X	—	X	—	—	—	—	—	—	—
Kormagnostus sp.	X	—	X	X	X	—	—	—	X	X
Homagnostus sp.	—	—	—	X	—	—	—	—	—	—
Pseudagnostus sp.	—	—	—	—	X	—	—	—	X	—
Pyg. undet. 2	—	—	X	—	—	—	—	—	—	—
Pyg. undet. 3	—	—	X	—	—	—	—	—	—	—
Acrothele	—	—	—	X	—	—	—	—	—	—
Opisthotreta sp.	—	X	—	X	X	—	X	—	—	—

much as Tremadocian faunas from the two regions are also similar. The inference is that those faunas of the Paleozoic tectonic belt existed under different environmental conditions than equivalent faunas on such shelf areas as the Llano Uplift.

A different fauna is represented by other boulders (types 5 and 6) which contain trilobites resembling those of the most complete development of the *Aphelaspis* zone of the eastern Llano Uplift; these are associated in the boulders with olenid trilobites (mainly *Parabolinella evansi* Kobayashi). Trilobites close to *Aphelaspis depressa* occur, as well as at least three other forms found with or above this species in the Lion Mountain member of the Riley formation. They include a fragmentary cranidium belonging to *"Taenicephalus" megalops* Kobayashi (1938b, p. 183, pl. 16, figs. 7–10, 35).

Evidently the same fauna was described by Kobayashi from stratigraphically unplaced collections made north of Jubilee Mountain in the Canadian Rockies of British Columbia by C. E. Evans. It has been referred to several times by Cambrian workers interested in interprovince correlation (Howell and Lochman, 1939, p. 119; Shaw, 1951, p. 100). It includes P 6/3 to P 6/8 (Kobayashi, 1938b, p. 154). Probably the three faunas named from Kobayashi's *Taenicephalus*, *Parabolinella* (black limestones), and *Megadunderbergia* (light gray limestone) are closely related, if not the same. The writer has not had the opportunity of examining these collections as they are at present in Japan. Seemingly, several of their separate species occur together: (1) in Woods Hollow boulder BM-4 (*Parabolinella evansi*, *"T." megalops*, and *Glyptagnostus reticulatus* with *Aphelaspis* cf. *A. walcotti*) and (2) in the highest *Aphelaspis* zone of the Lion Mountain member of the Riley formation in the Llano Uplift (*"Taenicephalus" longifrons* and closely allied forms to *Dunderbergia canadensis*, *D.* (*Megadunderbergia*) *quadrata*, and *D.* (*Megadunderbergia*) *convexa* Kobayashi).

This complete fauna needs restudy since it is a most important one for interprovince correlation. None of Kobayashi's species of *Taenicephalus* actually belong to that genus, and the stratigraphic position of the confused group *Dunderbergia* is now known from occurrences both in the western Cordillera of the United States and from Texas to be associated with or immediately below the *Elvinia* faunizone and not above it (compare Kobayashi's chart, 1938b, p. 160). The writer considers that all three of Kobayashi's faunas probably comprise parts of a single unit whose proper position is approximately that of the *Aphelaspis* zone but somewhat higher than the lowest occurrence of *A. walcotti*.

Boulders SS-26, SS-27, BM-2, and BM-new contain an olenid fauna more typical of the Atlantic province than that of boulder BM-4 whose species are now known only from the Cordilleran region. The key species of this fauna is Rasetti's *Parabolinella incerta* which occurs in all of the above boulders. Boulder BM-2 contains as well fragments of what may be *Olenus truncatus*, a cranidial fragment of a possible *Pterocephalina grata*, *Homagnostus obesus*, and *Pseudagnostus josephus*. All of these species except the last are also found in boulder BM-4 with *Aphelaspis* and *Parabolinella evansi*. The species *P. incerta* (Rasetti) was described originally (1945, p. 471) in exotic boulder A-3 of the Lévis and is there of Trempealeauan or Franconian age. In boulders SS-26 and SS-27 it occurs only with *Pseudagnostus* and an unidentified cranidium which resembles types common in North American faunas from the high *Aphelaspis* to middle Franconian beds. The writer conjectures that here *P. incerta* is of *Aphelaspis* zone age rather than younger, but the evidence is derived from scanty material and a relatively small fauna.

No trace of the prolific and widespread *Elvinia* fauna of North America has been found in the boulders. The *Elvinia* assemblage is probably of Cordilleran origin and spread eastward across the continent. It has never been found in the Appalachian trough beyond the western edge of the miogeosyncline (Wilson, 1952, p. 320) and is missing in the Lévis boulders of Quebec and in the Upper Cambrian sequence of northwestern Vermont. In the central Appalachians it is supplanted eastward by a different group of trilobites which the writer has termed the *Pseudosaratogia magna* fauna. Evidently, the *Elvinia* fauna did not reach into the Ouachita-Marathon belt of

clastic sedimentation. Howell and Lochman equate the upper limit of the *Elvinia* fauna with the *Olenus* zone of Scandinavia and its lower limit with the zones of *Lejopyge laevigatus* and *Agnostus pisiformis*. This is based on the occurrence in the *Elvinia* zone of *A. pisiformis*, *Homagnostus obesus*, and *Acrocephalites*. A restudy of the American specimens of *Acrocephalites* from Dinwoody Canyon, Wyoming (Howell and Lochman, 1939, p. 115), has shown that the form belongs to a new genus, *Cliffia* (Wilson, 1951, p. 632), and is rather different from the European *Acrocephalites*. The specimens of *Acrocephalites* stated by Howell and Lochman to be present in the *Irvingella major* zone of Wisconsin are now termed *Sulcocephalus* (Wilson and Frederickson, 1950, p. 897). This genus and its probable progenitor, *Berkeia*, are rather close to *Acrocephalites* and in spite of the renaming of American "*Acrocephalites*" to *Cliffia* the correlations of Howell and Lochman remain essentially correct, although Westergård's zone I (*Agnostus pisiformis*) is probably as old as the American *Aphelaspis* fauna. A fauna of lower Franconian age has long been known from the Russian island of Novaya Zemlya, and the species *Acrocephalites vigilans* Walcott and Resser was used to relate the fauna to the *Olenus* zone of Sweden. Frederickson (1949, p. 351) placed this species in his genus *Deckera*, a widespread member of the *Elvinia* fauna. This fauna contains a genus, *Pesaia*, allegedly quite close to *Elvinia* (Howell and Lochman, 1939, p. 116), but a recent and unpublished review of the type of *Pesaia* (by C. Lochman Balk, personal communication) has revealed little similarity between the two. The widespread genus *Irvingella* occurs in the Novaya Zemlya fauna and in general aspect the fauna approaches that of the North American province rather than that of the *Olenus* zone. The seemingly isolated occurrence of this North American fauna is best explained if the major faunas of the North American province are viewed as having a circumboreal distribution with contemporaneous olenid faunas existing only in or on the edges of geosynclinal belts where principally fine clastics and dark limestones were deposited around the northern continental shield (fig. 4).

The fact that no olenid genus has ever been found in North American strata of the *Crepicephalus* and *Cedaria* zones substantiates the opinion of Howell and Lochman (1939, pp. 118, 120) that these zones are probably unrepresented in the European sequence. Perhaps future study of the agnostid faunas of the Woods Hollow boulders will shed some light on these older Upper Cambrian correlations; at present, however, it appears that the oldest olenid faunas are of *Aphelaspis* zone age and that middle Franconian strata (*Conaspis* zone) of North America equate somewhere within Swedish zone III, the next above that of *Olenus* s.s. (II). Thus the first appearance of *Parabolina* (and its relative, *Parabolinoides*) coincides on both continents. This is checked rather well by the occurrence of the genus *Irvingella* which first appears in the *Elvinia* fauna but reaches its maximum development immediately above the same and in North America lingers on into the *Conaspis* fauna. In Sweden this form occurs in zone IIIa (subzone of *Orusia lenticularis*) and possibly also lower since it is associated as well with an *Olenus* type pygidium (Westergård, 1949).

Two boulders from widely separated localities in the Marathon Uplift (Bear Canyon and northwest of Garden Springs) contain fragmentary specimens of a middle Franconian fauna. *Pseudagnostus josephus* is abundant and species of *Taenicephalus*, *Wilbernia*, and *Bemaspis* occur. The material is too fragmentary for a large fauna to be recognized, but it makes clear that a rather different group of *Conaspis* zone trilobites existed on the continental edge of the Ouachita-Marathon facies belt. This fauna lacks olenid trilobites and is seemingly of North American affinity.

No Trempealeauan forms are known from any of the boulders, although the Franconian and Dresbachian are represented as well as the Lower Ordovician. Seemingly, the well-known saukiid trilobites are a typically North American shelf fauna whose contemporaries existing in the clastic belt are unknown.

An important fauna of earliest Ordovician age occurs in numerous boulders from both Simpson Springs and Bear Canyon localities (type 3). Its components include conodonts,

gastropods, ellesmeroceratid and baltoceratid nautiloids, but primarily trilobites. In addition to the writer's list, King (1937, p. 25) furnishes a faunal list from Simpson Springs Mountain boulders examined by E. O. Ulrich which includes:

Schizambon typicalis (Walcott)
Eoorthis desmopleura (Meek)
Symphysurina spicata (Ulrich)
Symphysurina, two n. spp.
Conokephalina inexpectans (Walcott)
Apatokephalus finalis
Hungaia ? sp.

Of the above species the writer has recognized only a *Symphysurina* and probably the *Apatokephalus* species which he has termed *A. serratus*. Ulrich's *Conokephalina inexpectans* (Walcott) is seemingly the species "*Dicellocephalus*" *inexpectans* Walcott, 1884, from the lower Pogonip of Eureka District, Nevada. This species was assigned to *Kainella* by Walcott in 1925 (p. 102). The writer has not collected *Kainella* from the boulders, but it is a well-established member of this fauna in the Cordilleran region and it is not surprising that it has been reported. The trilobites *Parahystricurus* and *Pseudohystricurus* relate this fauna to the early Canadian zones A-F of Ross's Garden City sequence. The species *Platycolpus capax* (Billings) has been described from the *Hungaia magnifica* fauna of the Lévis boulders (Franconian or Trempealeauan) indicating also a very early Canadian age for the Woods Hollow Ordovician boulders. The small specimen identified as *Rhombella* favors an age as high as Roubidoux (Bridge and Cloud, 1947, p. 551), and Dr. Rousseau Flower (personal communication) states tentatively that the baltoceratid cephalopods might be younger than Gasconade (Roubidoux to Black Rock) but could "not completely eliminate the Gasconade as a possibility."

The two European species *A. serratus* and *Parabolinella* cf. *P. triarthroides* Harrington mark middle or upper Tremadocian beds of England and Wales, 3a b–g members of the *Ceratopyge* beds of Sweden, and higher Tremadocian beds of Argentina.

The association of these trilobites with other trilobite, gastropod, and nautiloid genera of the North American area is a valuable aid to correlation. Apparently beds only as low as middle Tremadocian can be proved Gasconade in age, implying as suggested in 1939 by Howell and Lochman (p. 120) that the Trempealeauan may be in part of lower Tremadocian age.

The faunas in boulder type 3 are considered the same age as those discussed previously from the Marathon formation since here also a mixing of Gasconade trilobites and higher Tremadocian genera occurs. At present, however, not a single trilobite species occurs in both the boulders and the Marathon Tremadocian beds, but this is more likely the result of small collections and difference in biofacies than of appreciable difference in age.

Distribution of olenid trilobites in North America.—The following species of *Parabolinella* have been described from North America outside of the recognized Atlantic province faunas of Acadia:

1. *P. punctolineata* Kobayashi, 1936; beds of Franconian or Trempealeauan age, Alaskan-Yukon border.
2. *P. incerta* (Rasetti), 1945; Trempealeauan or Franconian boulder from Lévis conglomerate, Woods Hollow boulders (type 5), Marathon Uplift.
3. *P. triarthroides* Harrington, 1938; Tremadocian beds of the Gorge formation, northwestern Vermont (Shaw, 1951), and Tremadocian (lowest Ordovician) boulders of Woods Hollow (type 3), Goodwin limestone (Pogonip group), Monitor and Antelope Ranges, central Nevada.
4. *Parabolinella* sp. undet. *Aphelaspis* and *Elvinia* zones of Dunderberg formation, Nevada (personal communication by A. R. Palmer).

The following species differ from the above in having large palpebral lobes and thick anterior borders. They are closely related and quite possibly belong to an undescribed genus of olenid affinity.

5. *P. evansi* Kobayashi, 1936; isolated fauna in Canadian Rockies of British Columbia and *Aphelaspis* zone Woods Hollow boulders BM-4 and BM-8, Marathon Uplift, Texas.
6. *P. occidentalis* Wilson, 1951; *Conaspis*

zone of Ore Hill member, Gatesburg formation, Pennsylvania.

In addition, *Olenus* cf. *O. truncatus* has been identified in the Woods Hollow boulders and has been reported with *Glyptagnostus reticulatus* from the upper Conasauga formation at Cedar Bluff, Alabama. Kobayashi (1936b, p. 93) discounted Butts' *Olenus* identification and assigned the Alabama specimen to a new genus and species, *Proaulocopheura buttsi*, considering it non-olenid. Howell and Lochman (1939, p. 119) have pointed out a resemblance of this species to *Aphelaspis*. The writer examined the specimen in 1950 but came to no conclusion as to its affinities. The specimen is badly flattened in shale. Howell and Lochman suggested 13 years ago that this interesting locality of possible Atlantic province trilobites needs careful search and study, but the outcrop is reported to be completely obscured (Lochman Balk, personal communication).

So far as known, all olenid trilobites in North America both within and without the recognized Atlantic province occur in parts of the geosynclinal belts most removed from the foreland and commonly in dark argillaceous limestone sequences. Figure 4 suggests that the Scandinavian-English-Acadian belt continued down the Appalachian trend eastward of the miogeosynclinal Cambro-Ordovician deposits of the present folded Appalachians, followed the Ouachita trend through the southwest (Marathon area) and thence southward to connect with the northern Andean belt in Colombia (Harrington and Kay, 1951, p. 657). Connection of the Cordilleran belt of fine clastics and dark limestones with the Ouachita-Marathon belt is now obscured across northern Mexico, but all recognized olenid faunas of the Cordilleras bear the same relative position far into the geosyncline. It seems probable that the North American province so well differentiated in Middle and Upper Cambrian faunas is circumboreal in location and is bordered in the western hemisphere on the south and east by a circum-Atlantic province which as well followed the Cordilleran geosyncline northward to Canada and southward to the Andean belt.

Olenid faunas apparently appeared in these belts about *Aphelaspis* time and continued to evolve well into the Early Ordovician. From time to time as environmental situations favorable to this group opened up on or toward the shelf, various migrations of the group from the geosynclinal or clastic belts occurred in its direction. Thus forms either obviously olenid or derived from the group are now found at several stratigraphic horizons at widely separated localities. For example, *P. incerta* occurs in two instances in locally derived exotic boulders of miogeo-

EXPLANATION OF PLATE 24

FIGS. *1, 2, 7*—*Coosia pernamagna* Wilson, n. sp., *1*, dorsal view of cranidium, ×2, CW-245; *2*, dorsal view of cranidium, holotype, ×3, CW-246; *7*, dorsal view of paratype pygidium ×4, CW-247, all from boulder SS-24. (p. 267)

3, 22—*Nasocephalus flabellatus* Wilson, n. sp., *3*, dorsal view of holotype cranidium, ×3, CW-261; *22*, paratype free cheek, ×4, CW-263, both from boulder SS-31. (p. 269)

4, 5, 9—*Blountina* aff. *B. westoni* Rasetti, *4, 5*, dorsal and profile views of cranidium, ×3, CW-256; *9*, dorsal view of large pygidium, ×1, CW-255, both from boulder SS-24. (p. 267)

6—*Blountia ovata* Duncan, dorsal view of cranidium, ×5, CW-252, boulder SS-32. (p. 268)

8—*Kormagnostus* sp. undet., cranidium, ×6, CW-312, boulder SS-32. (p. 284)

10—*Coosia pernamagna* Wilson, n. sp. (?), dorsal view of possibly immature pygidium, ×4, CW-268, boulder SS-31. (p. 267)

11, 14, 18, 19, 21—*Nasocephalus nasutus* Wilson, n. sp., *11*, dorsal view of pygidium, ×3, CW-259; *14*, small cranidium with undetermined agnostid, ×3, CW-258; *18, 19*, profile and dorsal views of large cranidium, ×4, CW-257, holotype; *21*, dorsal view of free cheek, ×3, CW-260; all from boulder SS-32. (p. 269)

12—Undetermined pygidium 3, dorsal view, ×4, CW-250, from boulder SS-31. (p. 270)

13—Undetermined pygidium 1, ×3, CW-266, boulder SS-32. (p. 269)

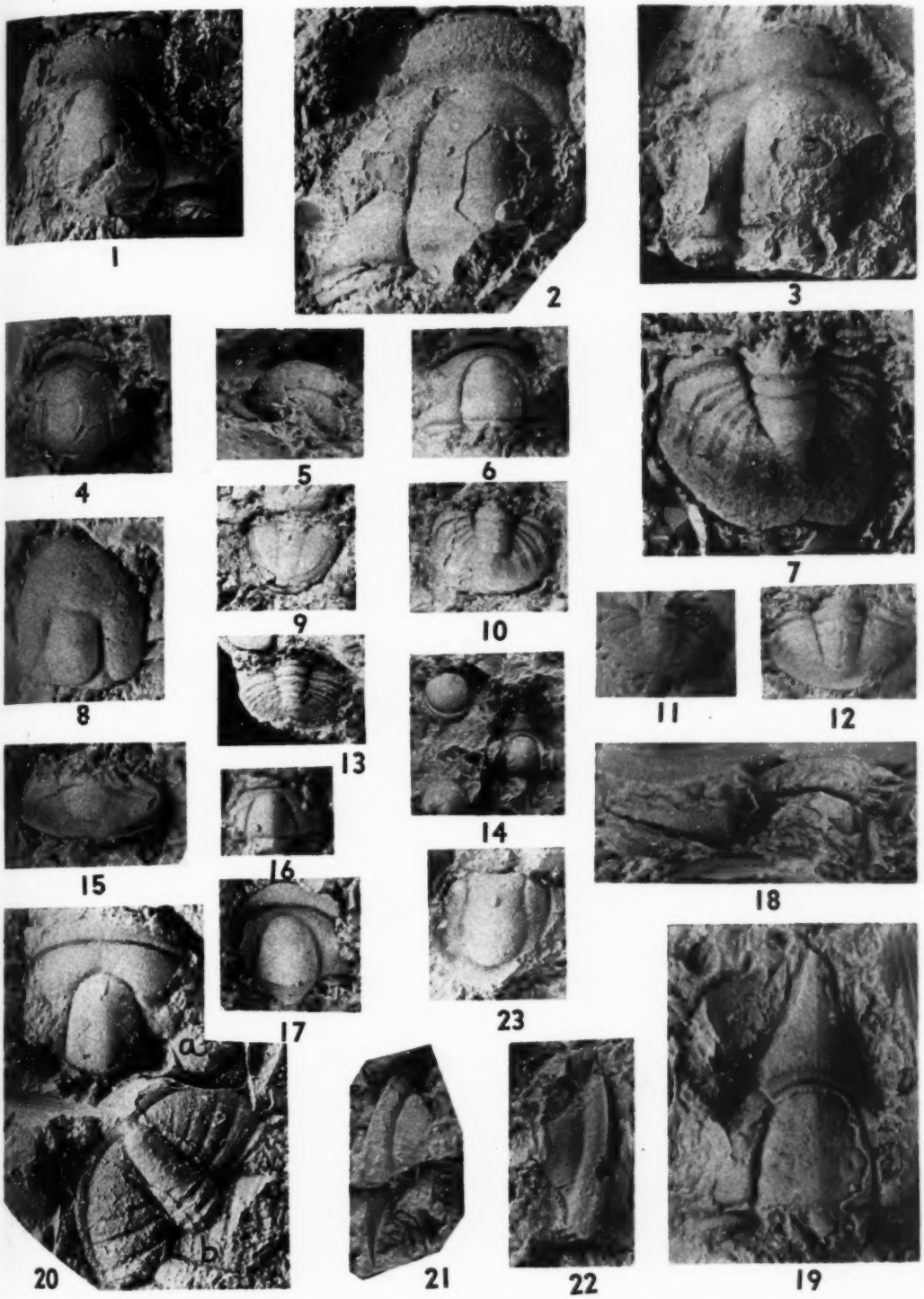
15—Undetermined pygidium 2, ×4, CW-267, boulder SS-31. (p. 270)

16—*Blountiella* sp. undet., dorsal view, ×5, of cranidium, CW-248, boulder SS-32. (p. 267)

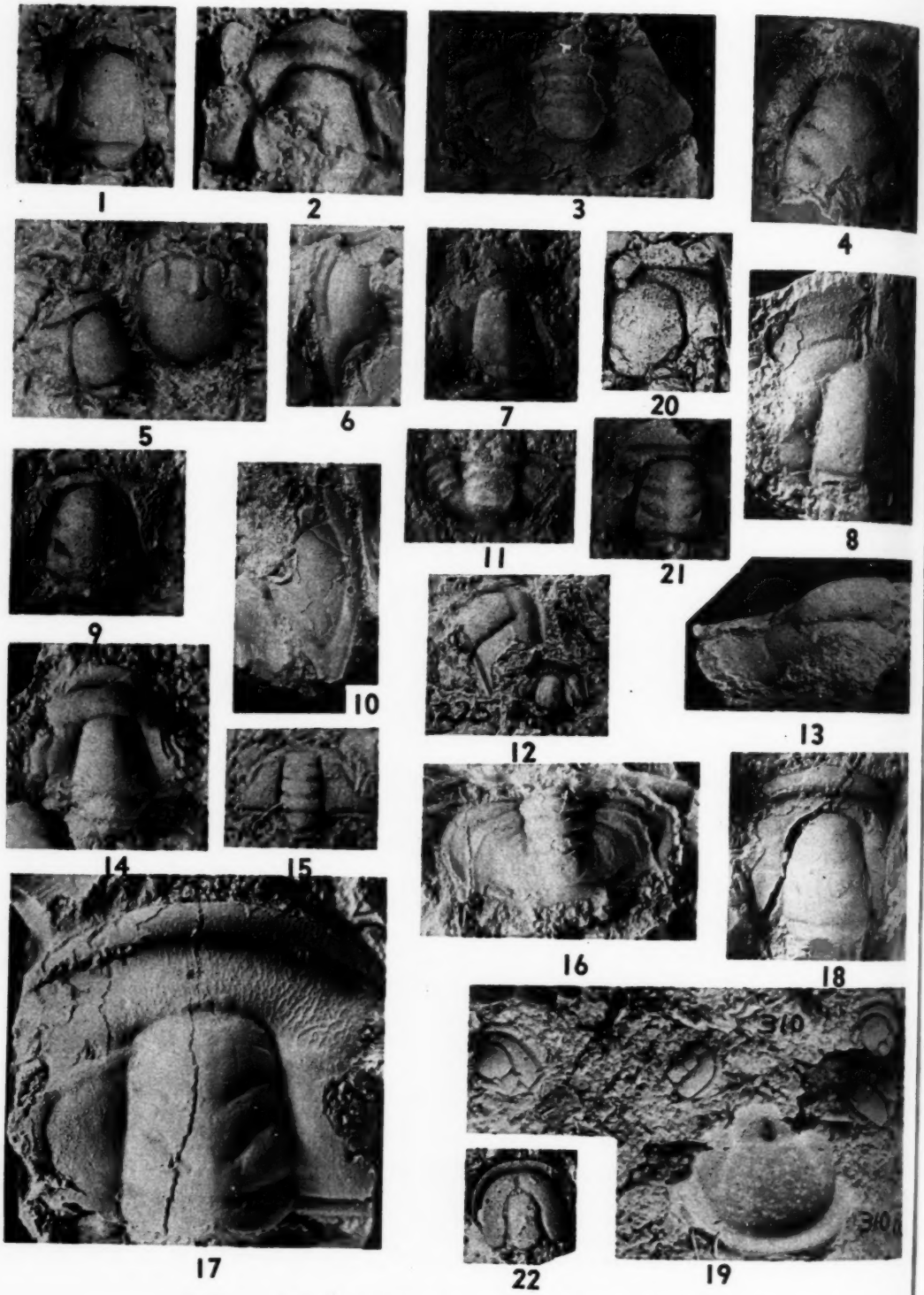
17—*Blountia assimilis* Resser, cranidium, ×7, CW-251 from boulder SS-31. (p. 268)

20—*Cedaria* aff. *C. gaspensis* Rasetti, dorsal view of cranidium and pygidium, ×3, CW-264a and b, boulder SS-33. (p. 269)

23—*Baltagnostus* sp. undet., pygidium, ×5, CW-304, Dresbachian boulder. (p. 284)



Wilson, Texas Cambrian and Ordovician trilobites



Wilson, Texas Cambrian and Ordovician trilobites

synclinal limestone facies and is of Trempealeauan or Franconian age (Lévis boulders) and according to present evidence probably also of Late Dresbachian age (Woods Hollow boulders). Probably part of the *Conaspis* fauna is olenid derived (*Parabolinoides* and *Bernia* of Frederickson, 1949; Raasch [unpublished material] reports *Parabolina* from this zone as well). Shaw's "*Terranovella*" of basal Ordovician (Tremadocian) age associated with an obvious olenid, *Parabolinella triarthroides*, is in the writer's opinion another olenid derivative. *Parabolinella* occurs in the western Cordillera evidently from *Aphelaspis* equivalent beds (A. R. Palmer, personal communication) through the Tremadocian. (*P. triarthroides* is reported from the lower Pogonip of central Nevada by L. F. Hintze (1953) and J. M. Greene, thesis manuscript, Columbia University.)

In the future, Late Cambrian and earliest Ordovician faunas in the interior parts of the southern Appalachian and Cordilleran troughs should become better known and serve to verify or disprove the implications made here that the early Paleozoic faunal provinces are in part facies controlled. Studies of the geosynclinal faunas are made difficult because they are now located in and on the edges of belts which have suffered orogeny several times in the Paleozoic beginning with the Medial Ordovician. Furthermore, paleoecologic studies of Cambrian trilobites, requisite to a full understanding of their distribution, have not yet been made.

SYSTEMATIC DESCRIPTIONS

North American Province Genera

GASTROPODA

Genus RHOMBELLA Bridge and Cloud, 1947

RHOMBELLA UMBILICATA (Ulrich & Bridge) ?

Plate 27, figure 4

Roubidouxia umbilicata ULRICH & BRIDGE, 1932, in Dake and Bridge, 1932, Geol. Soc. America Bull., vol. 43, p. 741, pl. 12, figs. 11, 12.

Rhombella umbilicata (Ulrich & Bridge), 1947, BRIDGE and CLOUD, Am. Jour. Sci., vol. 245, p. 550, pl. 1, figs. 14, 15; pl. 2, figs. 22, 24–26.

This small fragmentary gastropod shell agrees with Bridge and Cloud's description as far as the material permits observation. The apex is missing and the umbilical region cannot be observed. The depressed cone, profile view, estimated whorl number, and surface markings are those of *R. umbilicata*.

EXPLANATION OF PLATE 25

FIGS. *1, 5, 6*—*Wilbernia ? minuta* Wilson, n. sp., *1*, dorsal view of holotype cranidium, ×3, CW-238, boulder BC-2; *5*, dorsal view of paratype cranidium, CW-239, ×5, with pygidium of *Pseudagnostus josephus*, CW-309, boulder BC-2; *6*, free cheek, ×3, CW-237, boulder NWGS-6. (p. 273)

2—*Taenicephalus* sp. undet., dorsal view of cranidium, ×3, CW-233, boulder BC-2. (p. 271)

3, 11, 20—*Wilbernia* sp. undet., *3*, dorsal view of pygidium, ×3, CW-240, and *11*, dorsal view of pygidium, ×6, CW-315, possibly belonging to this genus; *20*, dorsal view of fragmentary cranidium, ×1.5, CW-227; all from boulder BC-2. (p. 273)

4, 9, 21—*Bemaspis dubita* Wilson, n. sp., *4*, dorsal view of paratype, ×3, CW-241; *9*, dorsal view of paratype, ×6, CW-242; *21*, dorsal view, ×6, CW-316, holotype; all cranidia and from boulder BC-2. (p. 272)

7, 12—Undetermined cranidia of *Aphelaspis* form, *7*, dorsal view, ×4, CW-224, with flatter frontal area and wider border than typical *Aphelaspis* species; *12*, small cranidium, ×3, with *A. walcotti*, CW-225a; both from boulder BM-4. (p. 270)

8, 13—*Pterocephalina* cf. *P. grata* Resser, dorsal and profile views, ×3, of cranidium, CW-220, boulder BM-4. (p. 271)

10, 15–17—*Parabolinella evansi* Kobayashi, *10*, free cheek, dorsal view, ×2, CW-231; *15*, meraspid cranidium, dorsal view, ×8, CW-228; *16*, dorsal view of pygidium, ×3.5, CW-229; *17*, dorsal view, of large cranidium, ×3, CW-230; all from boulder BM-4. (p. 281)

12, 14—*Aphelaspis* cf. *A. walcotti* Resser, *12*, oblique view from above of cranidium, ×3, CW-225; *14*, dorsal view, ×5, of less convex cranidium, CW-222; both from boulder BM-4. (p. 270)

18—*Aphelaspis* sp. undet., dorsal view of cranidium, ×3, CW-221, from boulder BM-4. (p. 270)

19—*Homagnostus obesus* (Belt), pygidia and cranidia, CW-310, and *Pseudagnostus cyclopyge*, CW-310a, pygidium, ×6, from boulder BM-4. (p. 284)

22—*Pseudagnostus josephus* (Hall), cranidium, ×5, dorsal view, CW-311, from boulder BC-2. (p. 284)

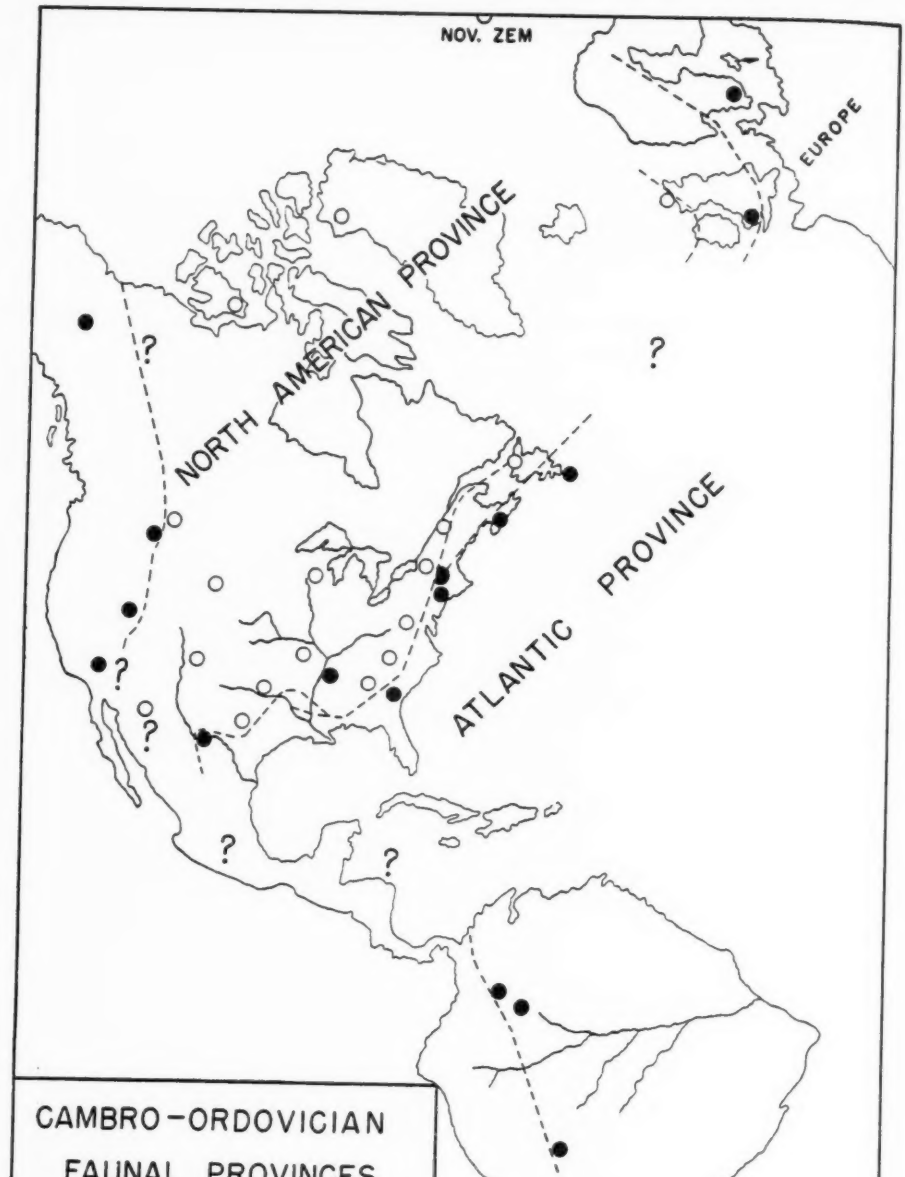


FIG. 4—Cambro-Ordovician faunal provinces in the western hemisphere relative to Paleozoic orogenic belts. The latter were depositional sites of dark argillites and calciargillites in the early Paleozoic.

The shell's maximum diameter is 15 mm.; height about 7 mm. One specimen only, known from boulder SS-30.

Figured specimen.—CW-201.

Genus SCHIZOPEA Butts, 1926
SCHIZOPEA sp. undet.
Plate 27, figure 15

A fragmentary internal mold is figured from boulder SS-30. The low spire and rounded whorl are typical. No surface markings visible.

Figured specimen.—CW-202.

TRILOBITA
Cedaria zone forms
Family ANOMOCARIDAE Poulsen, 1927
Genus COOSIA Walcott, 1916
COOSIA PERNAMAGNA Wilson, n. sp.
Plate 24, figures 1, 2, 7, 10

Coosia with glabella and occipital ring about three-fourths of total axial length of cranidium; glabella elevated and convex but frontal area flat, rather short compared to that of other species, except *C. robusta*. Border about four times axial length of brim, separated from it by a well-defined marginal furrow; border bears no secondary (false) marginal furrow. Fixed cheeks about one-fifth basal width of glabella, palpebral lobes on or anterior to center of glabella, relatively small for the genus. Most distinctive specific feature is broad back-curving posterior limbs.

Facial sutures cut anterior margin of cephalon away from axis, converge slightly anterior to eye and behind same trend outward obliquely at about 60° to longitudinal axis.

Pygidium almost quadrate, pleural platforms elevated and convex, axis half or less than half total axial length, bears three or four segments plus rounded terminal. Posterior border flat and unsegmented, marginal inbend present at axis.

Remarks.—The writer has used Palmer's manuscript diagnosis of the genus. *Coosia pernamagna* fits the *C. superba* characteristics except for the broad posterior limb, anterior position of the eye, and relatively shorter frontal area. It occurs in boulders SS-24, SS-31?, and SS-32.

Types.—Holotype cranidium, CW-246; paratype pygidium, CW-247; from SS-24.

Figured specimens.—Cranidium, CW-245, SS-24; pygidium, CW-268, from SS-31.

Family BLOUNTIIDAE Lochman, 1944
Genus BLOUNTIELLA Resser, 1938
BLOUNTIELLA sp. undet.
Plate 24, figure 16

A small (1.8 mm. long) fragmentary cranidium from boulder SS-32 is referred to this genus. This species is older than others of the genus which are known only from the *Crepicephalus* zone above the range of *Cedaria*.

Figured specimen.—Cranidium, CW-248, from SS-32.

Genus BLOUNTINA Lochman, 1944
BLOUNTINA aff. B. WESTONI Rasetti, 1946
Plate 24, figures 4, 5, 9

Blountina westoni RASETTI, 1946, Jour. Paleontology, vol. 20, p. 447, pl. 67, figs. 15, 16.

A single cranidium and possible associated pygidium show some similarity to Rasetti's species. Cranidium of moderate size (6.5 mm. long). Glabella and occipital lobe occupy over three-fourths total axial length. Cranidium as a whole and glabella very convex, occipital ring very faintly separated from latter; glabella in longitudinal profile rises above occipital lobe and anteriorly is steeply deflexed, defined by a very narrow dorsal furrow, slightly tapered and rounded anteriorly; no glabellar furrows. Frontal area deflexed, brim continuing the steep downslope of glabella but border almost horizontal. Ratio brim divided into border at axial length a little more than 1; both these features arcuate, border untapered laterally. Fixed cheeks steeply downsloping and narrow, ratio basal glabellar width divided into fixed cheek width a little more than 0.2; palpebral lobes very small flaps located about on midwidth line of glabella. Posterior limbs short and broad, steeply deflexed and deeply furrowed.

Anterior facial sutures cut margin well out from axis, very slightly convergent back to eye but trend posterolaterally about 60° with longitudinal axis.

Free cheek unknown.

The pygidium is assigned to this cranidium for it is the only blountiid type pygidium in the SS-24 collection large enough to fit. It is almost semicircular, only moderately con-

vex. A relatively narrow axis reaches down to marginal furrow and bears 8 to 9 segments.

Remarks.—This species is closest to *Blountina westoni* Rasetti but differs from it mainly in the medial position of the eye. It is much more convex than Rasetti's species, more so than most species assigned to the genus. It occurs in boulder SS-24.

Figured specimens.—Pygidium, CW-255; cranidium, CW-256.

Genus BLOUNTIA Walcott, 1916
BLOUNTIA ASSIMILIS Resser, 1938
Plate 24, figure 17

Blountia assimilis RESSER, 1938, Geol. Soc. America Special Paper 15, p. 64; pl. 12, fig. 33.

The very arcuate well-tapered and large border of this species makes assignment to Resser's sketchily described species probable. The ratio border divided by brim is from 1 to 2.5. The occipital ring extends backward axially. The fixed cheek width divided by basal glabellar width ratio is about 0.3 and the frontal area at axis divided by total axial length of cranidium is also about 0.3.

Occurrence.—The species occurs abundantly in boulder SS-31 and sparingly in SS-33.

Figured specimen.—Cranidium, CW-251, from SS-31.

BLOUNTIA OVATA Duncan, 1944
Plate 24, figure 6

Blountia ovata DUNCAN 1944, Geol. Soc. America Special Paper 54, p. 86, pl. 11, figs. 1–4.

This form agrees well with Duncan's description and is the most common type of *Blountia* present in the Dresbachian boulders, occurring in SS-32, SS-33, and SS-24. The occipital ring is not extended backward so far as in *B. assimilis* and the border is narrower. The marginal furrow bears a row of very faint pits. No pygidium is known for the species from any of the boulders.

Figured specimen.—Cranidium, CW-252 from SS-32.

Family CREPICEPHALIDAE Kobayashi, 1935
Genus NASOCEPHALUS Wilson, n. gen.*

Cranidium of moderate size (less than 1 cm. long), longer than wide, moderate relief to individual parts. Glabella prominent but not highly arched, rather depressed posteriorly but well defined by dorsal furrow which shallows anteriorly, well tapered and rounded anteriorly, with occipital ring occupying about two-thirds of axial length disregarding anterior spine; three pairs of very faint glabellar furrows, posterior two curved sharply backwards proximally; occipital ring projected backward axially, occipital spine may be present. Frontal area highly variable, brim very short but border projected anteriorly at axis. Fixed cheeks narrow (one-fourth to one-third basal glabellar width), elevated and convex, bearing well-marked obliquely backward trending ocular ridges and small semicircular palpebral lobes elevated above them and located about on the midwidth line through glabella; posterior limbs narrow and extended straight out, deeply furrowed.

Facial suture cuts anterior margin at long axis on non-spinose species, proceeds straight back to eye from anterolateral corners of cranidium, indents slightly behind same and trends straight out along posterior limbs.

A pygidium assigned questionably to one of the species of this genus is figured. It is convex, a little wider than long, with a large elevated axis bearing three segments and a terminal portion; pleural lobes well marked by two or three interpleural grooves which fade out posterolaterally; border lacking.

Remarks.—The genus is placed question-

* While this paper was in press Dr. A. H. Westergård (1953, pp. 3–6) published descriptions and illustrations of closely allied species to *Nasocephalus nasutus* and *N. flabellatus* from the high Middle Cambrian of Scandinavia (see addendum). These are assigned to *Agraulos*, the great variation of the border being considered an aberrant character not of generic significance. As Westergård points out Kobayashi (1935) and Lermontova (1940) agree with Frech (1897) in placing these forms in the genus *Proampyx*. The writer is in no position to discuss these European genera but is of the opinion that his species are congeneric with *Agraulos difformis* and *A. anceps*. The American species differ from those placed in *Agraulos* by Westergård in having a slightly less quadrate glabella, narrower, more elevated fixed cheeks, and possibly smaller eyes. All other features are the same including such details as the variations of the frontal limb, large occipital spine, and wide, well-marked glabellar furrows which are unusually clearly seen on internal molds.

ably in the Crepicephalidae because of similarities caused by the narrow elevated fixed cheeks and wide triangular or pointed border. The frontal limbs of the two species are somewhat similar to those of the *Dokimocephalus-Burnetia* species of the Franconian, yet basic characteristics of the glabella and fixed cheeks are so different as to deny any phylogenetic relation with this group. The flattened rather smooth glabella, narrow convex fixed cheeks, elevated palpebral lobes, and the bizarre border are distinctive features.

Type species.—*Nasocephalus nasutus* Wilson, n. sp.

NASOCEPHALUS NASUTUS Wilson, n. sp.
Plate 24, figures 11, 14, 18, 19, 21

The size range of the specimens (all from a single boulder) is from 5 to 10 mm. long. Almost half the cranidial length is formed by the border which is prolonged into a convex blunt spine. This is counter-balanced by a large thick occipital spine of about equal size although this is broken off all but one specimen. The test is finely tuberculate. The free cheek possesses a triangular ocular platform, steeply depressed laterally, a well-marked marginal furrow and a relatively wide, moderately convex border. Presumably the anterior facial suture cuts the margin of the cranidium at some place along the side of the cranidial spine. Occurrence is limited to boulder SS-32.

Holotype.—Cranidium, CW-257.

Figured specimens.—Cranidium, CW-258; pygidium, CW-259; free cheek, CW-260.

NASOCEPHALUS FLABELLATUS Wilson, n. sp.
Plate 24, figures 3, 22

The size range of the specimens is from 2 to 10 mm. long. A convex triangular border about four times the size of the axial length of the brim tapers sharply to the anterolateral corners of the cranidium. The occipital ring is slightly swollen posteriorly at the axis. Pygidium unknown. Free cheek similar to that of *N. nasutus*. Present in boulders SS-31 and SS-24.

Types.—Holotype cranidium, CW-261; paratype free cheek, CW-263; from SS-31.

Family CEDARIIDAE Raymond, 1937
Genus CEDARIA Walcott, 1925
CEDARIA aff. C. GASPENSIS Rasetti, 1946
Plate 24, figure 20

This species is represented by thousands of cranidia and pygidia in one large boulder (SS-33) and occurs sporadically in others. The rounded glabella distinguishes it from the Rocky Mountain species described by Lochman and Duncan (1944) and it does not resemble much the *Cedaria* species known from the Hickory member of the Riley formation of the Llano Uplift in Texas. Unfortunately no posterior limb was seen in the fragments of the coquina in boulder SS-33. The following tabulation distinguishes the species from the typical *C. gaspensis* of the Lévis conglomerate.

The species occurs in the following boulders: SS-24, SS-29, SS-32, SS-33, SS-34, SS-35, SS- small unnumbered. Fragments of *Cedaria* probably belonging to this species occur in other boulders from Simpson Springs and Bourland Mountain localities.

Figured specimen.—Cranidium and pygidium, CW-264, from SS-33.

Undetermined pygidium 1
Plate 24, figure 13

Pygidium about twice as wide as long. Axis less than one-third total width, well-defined and convex, although pygidium as a whole is flat; about five axial segments. Distinctive feature is segmentation of gently

TABLE 3.—COMPARISON WITH TYPICAL *Cedaria gaspensis*

C. gaspensis, Lévis conglomerate	*Cedaria* aff. *C. gaspensis*, Boulder SS-33
a. Palpebral lobes slightly anterior of mid-width of glabella	a. Palpebral lobes medial
b. Punctae in marginal furrow	b. Faint punctae in marginal furrow
c. 8 or 9 segments on pygidial axis 7 or 8 segments on pleural lobes	c. 6 plus segments on pygidial axis 5 or 6 segments on pleural lobes
d. Pygidium 2¼ times wider than long	d. Pygidium 2 times wider than long

convex pleural platforms. Three or four segments are marked with both pleural and interpleural grooves. No well-defined border exists; segmentation extends to lateral margins but fades out posteriorly.

Figured specimen.—CW-266 from SS-32.

Undetermined pygidium 2
Plate 24, figure 15

Small pygidium much wider than long, very convex with large axis occupying about one-third total width and showing three faint segments and a terminal lobe reaching to posterior margin axially. Pleural platforms show only one anterior-most segment; anterior margins round and slope back to small sharp posterolateral corners; posterior margin relatively straight. No real border present. Present in boulders SS-31 and SS-32.

Figured specimen.—CW-267 from SS-31.

Undetermined pygidium 3
Plate 24, figure 12

Pygidium about twice as wide as long, moderately convex. Axis almost as wide as pleural platforms, well-tapered, extended to border, marked by five segments and a terminal; a flat horizontal border completely encircles lateral and posterior margins. Occurs in boulder SS-31.

Figured specimen.—CW-250, SS-31.

Aphelaspis zone trilobites
Family undetermined
Genus APHELASPIS Resser, 1935

APHELASPIS cf. A. WALCOTTI Resser, 1938
Plate 25, figures 12, 14, plate 26, figure 17

Aphelaspis depressa RESSER, 1935, Smithsonian Misc. Coll., vol. 93, no. 5, p. 11. (Not considered synonymous with *Conocephalites depressus* Shumard 1861.)

Aphelaspis depressus BRIDGE, 1936, U. S. Geol. Survey, Prof. Paper 186, p. 255, pl. 69, figs. 23–26. (Not considered synonymous with *C. depressus* Shumard 1861.)

Aphelaspis walcotti RESSER, 1935, Geol. Soc. America, Special Paper 15, p. 59; pl. 13, fig. 14.

Aphelaspis depressa NELSON, 1951, Jour. Paleontology, vol. 25, p. 774; pl. 106, fig. 14. (Not considered synonymous with *C. depressus* Shumard 1861.)

Aphelaspis walcotti Resser, PALMER, 1953, Jour. Paleontology, vol. 27, p. 157. (Transfer of specific concept from *C. depressus* Shumard, 1861, to *A. walcotti* Resser.)

Four small cranidia (about 4.5 mm. long) occur in boulders BM-4 and BM-8. These resemble small specimens of *A. walcotti* closely except that they possess large palpebral lobes whose length is greater than one-fourth the total cranidial length.

Figured specimens.—Cranidia, CW-223, CW-222, CW-225, from BM-4.

APHELASPIS sp. undet.
Plate 25, figure 18

A single cranidium from boulder BM-4 resembles additional material from the upper Lion Mountain member of the Riley formation in the Llano Uplift (higher *Aphelaspis* zone). Cranidium elongate (8.5 mm. long), moderately convex with considerable relief to individual parts. Glabella long, convex, well defined, with tapered rounded front, with occipital ring occupying more than two-thirds of cranidial length; possesses three faint pairs of oblique glabellar furrows. Border convex, evenly tapered distally from axis, axially a little larger than brim which is deflexed; ocular ridge pronounced, palpebral lobe large, crescentic and medially located; fixed cheeks flat, about one-third basal glabellar width; posterior limb unknown.

Facial suture intramarginal to axis, from anterolateral corners trends slightly inward; posterior courses unknown.

Pygidium and free cheek unknown.

Remarks.—Boulder BM-4 contains almost as great a variety of *Aphelaspis* as the zone by that name in the Riley formation but accurate distinction between the forms cannot be made on such scanty material obtained from unmeasured sections. When the Llano Uplift faunas of this age are more fully described by A. R. Palmer (manuscript now in press) and the Dunderberg shale faunas are better known, more definite names can be applied to many of the species from boulders BM-2, BM-4, and BM-8 and Kobayashi's "*Taenicephalus*," *Megadunderbergia*, and *Parabolinella* faunas can be fitted into proper stratigraphic position.

Figured specimen.—Cranidium, CW-221 from BM-4.

Other figured specimens of *Aphelaspis* affinities from the same boulders:

CW-225a, Pl. 25, fig. 12: small cranidium, immature(?) from BM-4.

CW-224, Pl. 25, fig. 7: like CW-221 but with a

flatter frontal area and relatively wider border. CW-232, Pl. 26, fig. 27: pygidium like that assigned by Kobayashi (1938, p. 184, pl. 16, fig. 26) to "*Taenicephalus*" *longifrons* except that it has two less axial segments.

Genus PTEROCEPHALINA Resser, 1938

PTEROCEPHALINA cf. P. GRATA Resser, 1942

Plate 25, figures 8, 13; plate 26, figure 1

Pterocephalina grata RESSER 1942, Smithsonian Misc. Coll., vol. 103, no. 5, p. 78; pl. 15, figs. 3–6.

Several fragments of cranidia close to Resser's species exist in boulders BM-2 and BM-4. *Pterocephalina* species are also present in the Llano Uplift *Aphelaspis* zone but as yet are undescribed except for a pygidium figured by Resser (1942, p. 76, pl. 14, figs. 32, 33).

Cranidium elongate and moderately convex, furrows shallow; no elevation on cranidium except that of glabella which with occipital ring occupies one-half to two-thirds of total cranidial length and is cylindrical, rounded frontally, and faintly keeled axially; glabellar furrows oblique and very faint. Border and brim flat, widely concave with a very shallow and narrow marginal furrow, border about twice the brim size at midlength; fixed cheeks one-third or less basal glabellar width, flat or gently downsloping, ocular ridges faint; palpebral lobes and posterior limb unknown.

Facial suture intramarginal to axis, very slightly directed inward toward palpebral lobes; posterior course unknown.

Figured specimens.—Cranidium, CW-220; from BM-4; cranidium, CW-227 from BM-2.

"TAENICEPHALUS" MEGALOPS
Kobayashi, 1938
Plate 26, figure 28

Taenicephalus megalops KOBAYASHI, 1938, Japanese Jour. Geol. Geogr., vol. 15, nos. 3–4, p. 183, pl. 16, figs. 7–10.

A single cranidium is figured which is almost identical with forms discovered by A. R. Palmer (in press) in the uppermost *Aphelaspis* zone of the Lion Mountain member of the Riley formation, Llano Uplift. It is strikingly similar to the species *T. megalops* Kobayashi but differs greatly from any form now construed as belonging in the genus *Taenicephalus*. In fact, in the writer's opinion, none of Kobayashi's *Taenicephalus* species of 1938 are members of that genus but with other forms from his *Taenicephalus, Dunderbergia,* and *Megadunderbergia* limestone faunas indicate a lower stratigraphic level and are very like undescribed species from the higher *Aphelaspis* zone of the Llano Uplift and boulder BM-4 from the Marathon region. This species probably belongs to a new genus but it should be described from the abundant and stratigraphically placed material in the Lion Mountain rather than on the basis of fragments from poorly known or out-of-place strata.

Cranidium of the specimen moderately convex with fairly high relief to individual parts. Glabella large and elevated, with occipital ring occupying more than two-thirds of cranidial length, tapered and rounded anteriorly; dorsal furrow well incised with pits at anterolateral corners of glabella, posterior pair of glabellar furrows well-defined and oblique, other pairs faint or absent. Border convex and tapered laterally, slightly swollen and enlarged posteriorly at axis, less than half size of brim which is flat and deflexed: fixed cheeks slightly arched, just less than half width of glabellar base, ocular ridge faint; posterior limb and palpebral lobe unknown but position of latter is probably medial.

Free check and pygidium unknown.

Figured specimen.—Cranidium, CW-226 from BM-4.

Middle Franconian trilobites
Genus TAENICEPHALUS Ulrich & Resser, 1925
TAENICEPHALUS sp. undet.
Plate 25, figure 2

Fragments of cranidia from boulders NWGS-6 and BC-2 indicate a species of *Taenicephalus* with the high relief and extreme triangular border of western species of the genus. Cranidium depressed but with very deep furrows. Glabella with occipital ring about two-thirds total cranidial length, sharply tapered and truncate with three pairs of normally impressed oblique furrows; dorsal furrow wide and deep with very deep pits at anterior glabellar corners. Border triangular, fully as large as brim at axis, marginal furrow wide and deep;

fixed cheeks narrow and elevated with rather large palpebral lobe completely anterior to center of glabella. Posterior limb unknown but deeply furrowed.

A pygidial fragment (unfigured) shows a typically large axis with two axial segments plus a terminal portion and faintly furrowed pleural platforms.

Figured specimen.—Cranidium, CW-233 from BC-2.

Genus BEMASPIS Frederickson, 1949

BEMASPIS DUBITA Wilson, n. sp.

Plate 25, figures 4, 9, 21

Cranidium moderately convex, with well-defined relief to individual parts, much wider than long. Glabella slightly more than two-thirds length of cranidium, convex, keeled, truncate-rounded anteriorly; three pairs of well-incised, rather wide furrows although anterior pair is faint; occipital furrow and ring well defined, with a well-developed occipital node (or perhaps a short spine); dorsal furrow well defined, wider lateral to glabella than anteriorly. Brim slightly convex, marginal furrow deep and slightly arcuate, border slightly convex, lying in same horizontal plane as brim, not quite twice size of brim at axis, tapering laterally. Fixed cheeks one-fourth basal width of glabella, elevated and convex; small round palpebral lobes located anterior to glabellar center, opposite second pair of glabellar furrows, elevated above fixed cheek and joined by a well-defined very oblique ocular ridge. Posterior limbs poorly pre-

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EXPLANATION OF PLATE 26

FIG. *1*—*Pterocephalina* cf. *P. grata* Resser, dorsal view of interior mold of cranidium, ×3, CW-227, boulder BM-2. (p. 271)

2, 4, 5, 7, 10—*Beltella latifrons* Wilson, n. sp., *2*, dorsal view, of holotype cranidium, ×3, CW-281; *4*, dorsal view of fragmentary cranidium, ×5, CW-284; *5*, paratype free cheek, ×3, CW-286; *7*, dorsal view of cranidium, ×4, CW-283; *10*, dorsal view of paratype pygidium, ×3, CW-288; all from coll. 4, 4 mi. SW Marathon, basal Marathon formation. (p. 277)

3, 6—*Andesaspis argentinensis* Kobayashi, *3*, imperfect cranidium, ×3, CW-289, coll. 4, 4 mi. SW Marathon; *6*, dorsal view of cranidium, ×3, CW-290, from coll. 2, 4 mi. SW Marathon; both from basal Marathon formation. (p. 279)

4—*Tostonia* sp. undet., dorsal view of pygidium with cranidium of *Beltella latifrons*, ×5, CW-285, coll. 4, 4 mi. SW Marathon, basal Marathon formation. (p. 279)

8—*Shumardia* sp. undet., dorsal view of cranidium with outlines accentuated, ×10, CW-291, RR rd. 1.5 mi. south, basal Marathon or upper Dagger Flat formation. (p. 275)

9—Subfamily Asaphinae, forked hypostome, exterior (ventral) view, ×4, CW-278; coll. A, RR rd. 1.1 mil. south. (p. 284)

11—*Pseudagnostus bilobus* Shaw, dorsal view of pygidium, ×5, CW-298, coll. 4, 4 mi. SW Marathon, basal Marathon formation. (p. 284)

12—*Parahystricurus* sp. undet., fragmentary cranidium, dorsal view, ×6, CW-203, boulder SS-36. (p. 274)

13—*Pseudagnostus cyclopyge*, oblique dorsal view of cranidium, ×6, CW-313b, boulder BM-4. (p. 284)

14, 16—*Geragnostus* sp. undet., *14*, dorsal view of pygidium, ×5, CW-300; *16*, dorsal view of fragmentary cranidium, ×5, CW-299; both from coll. A, RR rd. 1.1 mi south. (p. 284)

15—*Pseudohystricurus* sp. undet., dorsal view of cranidium, ×4, CW-305, boulder SS-37. (p. 274)

17—*Aphelaspis* cf. *A. walcotti* Resser, dorsal view of cranidium, ×3, CW-223, boulder BM-4. (p. 270)

18–22—*Parabolinella incerta* (Rasetti) *18*, dorsal views of cranidium and free cheek, ×3, CW-216b and c; *19*, dorsal view of cranidium, ×3, CW-218; *20*, fragmentary cranidium and free cheek, ×3, CW-216; *21*, best cranidium, ×4, CW-214; *22*, free cheek fragmentary pygidium sp. undet. 5, and undetermined cranidium, ×3, CW-216a. (p. 280)

23—*Homagnostus obesus* (Belt), pygidium and cranidium, ×6, CW-313a, boulder BM-4. (p. 284)

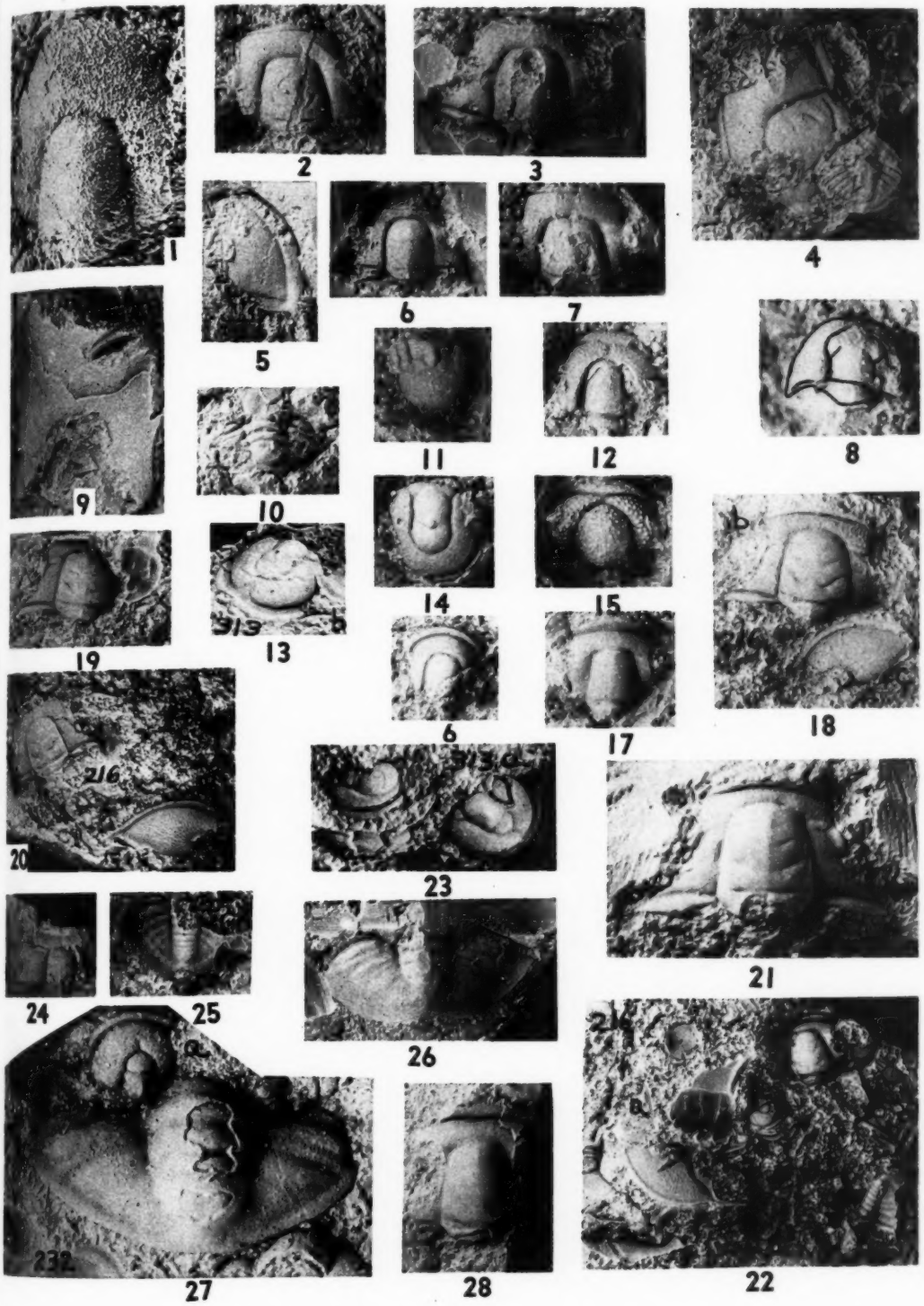
24—*Olenus* cf. *O. truncatus* (Brünnich), dorsal view of small fragmentary cranidium, ×5, CW-212, boulder BM-2. (p. 282)

25—Pygidium, sp. undet. 5, dorsal view, ×5, CW-215, boulder SS-26. (p. 282)

26—Pygidium sp. undet. 4, dorsal view, ×2, CW-213, boulder BM-4. (p. 282)

27—Pygidium possibly belonging to "*Taenicephalus*" *longifrons* Kobayashi, dorsal view, ×6, CW-232, with cranidium of *Homagnostus obesus* (Belt), CW-232a; boulder BM-4. (p. 284)

28—"*Taenicephalus*" *megalops* Kobayashi, dorsal view of fragmentary cranidium, ×2, CW-226, boulder BM-4. (p. 271)



Wilson, Texas Cambrian and Ordovician trilobites

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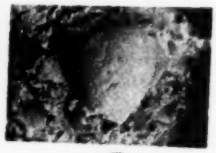
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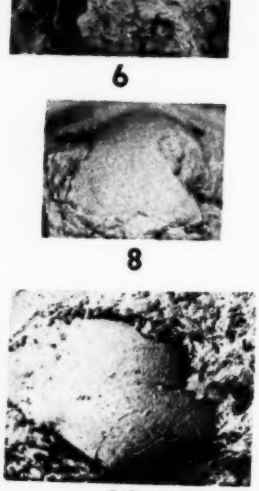
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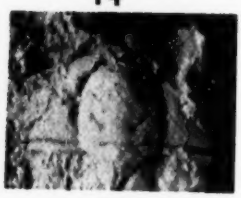
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Wilson, Texas Cambrian and Ordovician trilobites

served but evidently rather broad and triangular. Free cheek unknown. Facial suture as in type species.

Remarks.—The writer's specimens have been compared with plaster casts of Frederickson's type species. The cranidia are 3 or 4 mm. long and smaller than the Oklahoma specimens. They differ from this species in having narrower, more convex fixed cheeks, and a wider, less laterally tapered border.

Types.—Holotype cranidium, CW-316; paratype cranidia, CW-241 and CW-242; all from BC-2.

Genus WILBERNIA Walcott, 1925

WILBERNIA sp. undet.

Plate 25, figures 3, 11, 20

The anterior half of one large cranidium is present and shows a brim-border ratio of 1 and comparatively strong glabellar furrows. In these features it most resembles *W. halli* Resser. The elongate cylindrical glabella and comparatively flattened cranidium of the genus are demonstrated by the specimen. The fixed cheeks are more elevated and the palpebral lobes are more anteriorly located and shorter than in other species.

A possible pygidium, assigned merely because of association, is large, slightly wider than long with a thick elevated axis bearing three rings and a terminal segment and reaching not quite to a flat narrow border; oblique pleural and interpleural grooves are rather well defined.

Figured specimens.—Cranidium, CW-227; pygidia, CW-240 and CW-315; all from BC-2.

WILBERNIA ? MINUTA Wilson, n. sp.

Plate 25, figures 1, 5, 6

Cranidium moderately convex with moderate relief, furrows narrow but well defined, small, specimens ranging from 3 to 8 mm. long. Glabella large, convex, well defined, cylindrical with rounded front and rather faint oblique furrows, the posteriormost pair faintly connected horizontally across glabellar axis. Border up-arched but lying in horizontal plane, thick and evenly tapered; widely arcuate, faintly pitted; a deep marginal furrow passes immediately in front of glabella so that a brim is absent on smallest cranidia and very narrow on larger ones. Fixed cheeks narrow (about one-fourth of basal glabellar width), elevated with small thick palpebral lobes just posterior to midwidth of glabella. Occipital ring separated by well-defined furrow, arched

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EXPLANATION OF PLATE 27

FIGS. *1, 2, 13*—*Apatokephalus serratus* (Sars & Boeck), *1*, dorsal view of free cheek, ×4, CW-211; *2*, dorsal view of cranidium, ×3, CW-209; *13*, dorsal view of pygidium, ×4, CW-210; all from boulder SS-36. (p. 275)

3, 11—*Asaphellus* sp. undet., *3*, dorsal view of cranidium, ×2, CW-271, coll. 3, 4 mi. SW Marathon; *11*, dorsal view of cranidium, ×4, CW-272, RR rd. 1.1 mi. south, coll. B. (p. 283)

4—*Rhombella umbilicata* (Ulrich & Bridge) ?, profile view, ×4, CW-201, boulder SS-30. (p. 265)

5–8—*Platycolpus* cf. *P. capax* (Billings), *5*, exterior (ventral view) of hypostome, ×4, CW-307; *6–8*, profile, dorsal and frontal views of cranidium, ×3, CW-200; all from boulder SS-38. (p. 274)

9, 19—*Bellefontia* sp., *9*, cranidial fragment cf. *B. acuminiferentis* Ross, dorsal view, ×4, CW-276; *19*, dorsal view of pygidium, ×4, CW-277; both from coll. A, RR rd. 1.1 mi. south. (p. 284)

10, 14—*Symphysurina* cf. *S. woosteri* Ulrich, *10*, dorsal view of fragmentary cranidium, ×4, CW-279; *14*, dorsal view of clay mold of cranidium, ×4, CW-280; both from coll. 4, 4 mi. SW Marathon. (p. 284)

12—Genus and species undet., dorsal view of fragmentary cranidium, ×7, CW-292, RR rd. 2.8 mi. (p. 275)

15—*Schizopea* sp. undet., apical view of internal mold of shell, ×3, CW-202, from boulder SS-30. (p. 267)

16, 17, 20—*Trigonocerca* sp. undet., *16, 17*, dorsal and profile views of pygidium, ×2, CW-270; *20*, dorsal view of pygidium, ×2, CW-269; both from coll. 3, 4 mi. SW Marathon. (p. 283)

18—*Parabolinella* cf. *P. triarthroides* Harrington, dorsal view of fragmentary cranidium, ×4, CW-208, boulder SS-36. (p. 280)

21—Asaphid pygidium, sp. undet., dorsal view, ×4, CW-275, coll. A, RR rd. 1.1 mi. (p. 284)

backward somewhat, well tapered laterally and with a small occipital node.

The free cheek cannot be certainly assigned to the cranidium, but the facial suture outlines agree. Ocular platform well arched, marginal furrow distinct but a little shallower than the cranidial structure would suggest, becoming indistinct near genal spine which is rather blunt.

Remarks.—This species may be superficially compared with *Comanchia amplooculata* Frederickson, but it differs in having less impressed glabellar furrows, smaller and less posteriorly placed palpebral lobes, and a thick convex border rather than a flat expanded one. The cranidium is also on an average much larger than that of the *Comanchia* species.

The species is assigned with some hesitation to the genus *Wilbernia*, but the size and position of the palpebral lobes, the large cylindrical glabella, narrower fixed cheeks, and characteristic faint pits in the marginal furrow seem to show its affinity. The straightness of the marginal furrow, thick border, and general narrowness of the brim differ from the general concept of *Wilbernia* but the present range of variation in the genus encompasses these characteristics. The main difference noticed is the very convex glabella of *W.* ? *minuta* although the cranidium as a whole is not particularly convex. The possibility cannot be overlooked that these forms represent small holaspid cranidia with somewhat different proportions than the large mature form. About six specimens were observed in the collections from boulders NWGS-6 and BC-2.

Types.—Holotype cranidium, CW-238; paratype cranidium, CW-239; both from BC-2.

Figured specimen.—Free cheek, CW-237, from NWGS-6.

Lower Ordovician trilobites from North American Province

Family unknown

Genus PARAHYSTRICURUS Ross, 1951

Plate 26, figure 12

Two fragmentary depressed cranidia probably represent a new species of Ross's genus (1951, p. 56). Proportions on the cranidia, particularly the cylindrical glabella, resemble those of *P. pustulosa* Ross. The specimens differ from all other species of the genus in the extreme posterior position of the palpebral lobes which, although typical of the genus in their smallness, are located opposite the base of the glabella.

No free cheek or pygidium known.

The specimens occur in boulder SS-36 with *Parabolinella* cf. *P. triarthroides* and *Apatokephalus serratus*.

Figured specimen.—Cranidium, CW-203 from SS-36.

Genus PSEUDOHYSTRICURUS Ross, 1951

PSEUDOHYSTRICURUS sp. Ross, 1951

Plate 26, figure 15

Pseudohystricurus sp. Ross, 1951, Peabody Mus. Nat. Hist., Yale Univ. Bull. 6, p. 75; pl. 16, figs. 26, 27, 31.

Two fragmentary cranidia about 4 mm. long of *Pseudohystricurus* occur in boulder SS-37. They lack posterior limbs and palpebral lobes but resemble strongly a species described but not named by Ross from "zone E" of the Garden City limestone. The material suggests moderate-sized palpebral lobes located anterior to the glabella center and the brim contains a well-marked axial furrow. The width of the fixed cheeks is about one-third the basal glabellar width. Additional fragments in boulders SS-38 and SS-30 indicate that possibly a different species of the genus exists in these collections.

Figured specimen.—Cranidium, CW-305 from SS-37.

Genus PLATYCOLPUS Raymond, 1913

PLATYCOLPUS cf. P. CAPAX (Billings), 1860

Plate 27, figures 5–8

Platycolpus capax (Billings), RASETTI, 1944, Jour. Paleontology, vol. 18, p. 250; pl. 39, figs. 1–12 (complete synonymy).

The palpebral lobes, shape and size of the glabella, frontal area, and posterior limbs are very similar in this species and *P. capax*. The width of the fixed cheeks is approximately the same. The species differs from *P. capax* in having a slightly keeled glabella and seemingly fainter occipital and marginal furrows. Its border is less well defined, narrower, and more downturned beneath the glabella than in the Lévis boulder species.

The cranidium somewhat resembles *Symphysurina* sp. A Ross (1951, p. 115, pl. 28, figs. 29, 31–36) in the well-defined course of the dorsal furrow and in general proportions, but has smaller, better defined palpebral lobes and a better defined marginal furrow.

No pygidium or free cheek is present with the two cranidia discovered in boulder SS-38 but a possible hypostome from the same boulder is figured. It resembles that of *Symphysurina* (*Symphysuroides minima* Shaw 1951, p. 107, pl. 21, fig. 17).

Figured specimens.—Cranidium, CW-200; hypostome, CW-307; from SS-38.

Atlantic Province trilobites
Family CONOCORYPHIDAE Angelin, 1854
Genus and species undet.
Plate 27, figure 12

Despite the distinctive form of this fragmentary cranidium a search of the literature reveals only that it must belong to the family which includes *Elyx* Angelin, 1851. *Ctenocephalus* Corda, 1847, and *Dasometopus* Resser, 1936—all Middle Cambrian genera.

The fragment most closely resembles *Elyx laticeps* (Angelin) (Westergård, 1950, p. 32, pl. 7, figs. 1–5) in its pustulose test, preglabellar boss and straight anterior margin. The boss differs from that of *Elyx* in being disconnected from the border. It also differs in its poorly defined border, in the obsolescence of the glabellar furrows, the two pairs of which are reduced to deep pits, and in having a shorter glabella. The occipital lobe is triangular, posteriorly extended, and evidently bears a large dorsally projected spine. Lateral margins of the cranidium are uncertainly known and are possibly broken off the specimen.

The form resembles *Deiracephalus* Resser, 1935, to some extent but differs from it in its narrower fixed cheeks, anteriorly fading boss and deep pit-like glabellar furrows.

In its border it more resembles *Dasometopus* (Westergård, 1950, p. 35, pl. 8, figs. 1–3) but the cranidial shape and proportionate length and width of the glabella and cranidium differ. These differences are not surprising as the specimen is from younger strata than the seemingly related genera. It was found by V. E. Barnes in lowermost Marathon beds (Tremadocian) in the measured section at RR rd. 2.8 mi. south, just above collection 2. The shape and proportions of the glabella distinguish this genus from *Loganopeltis* and *Loganopeltoides* which it superficially resembles and which also occur in Lower Ordovician beds.

Figured specimen.—Cranidium, CW-292, from RR rd 2.8 mi. south.

Family SHUMARDIIDAE Lake, 1907
Genus SHUMARDIA Billings, 1865
SHUMARDIA sp. undet.
Plate 26, figure 8

One cranidium was collected from badly distorted beds probably high in the Dagger Flat formation along Roberts ranch road 1.1 mile south of Alsate Creek. The cranidium resembles that of *S. pusilla* (Sars) (Lake, 1907, p. 40, pl. 3, figs. 18–20; pl. 4, figs. 1–4) in relative width and shape of the glabella and in the size and degree of definition of the peculiar lateral lobes. It lacks any trace of horizontal glabellar furrows. The dorsal furrow shallows anteriorly; the anterior end of the glabella is bluntly acuminate.

Figured specimen.—Cranidium, CW-291, RR rd. 1.5 mi. south.

Family REMOPLEURIDAE Hawle & Corda, 1847
Genus APATOKEPHALUS Brögger, 1897
APATOKEPHALUS SERRATUS (Sars & Boeck), 1838
Plate 27, figures 1, 2, 13

Apatokephalus serratus (Boeck), RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1084.
Apatokephalus serratus (Sars & Boeck), HARRINGTON, 1938, Revista del Mus. Plata (nueva serie), Tm. 1, Paleont., no. 4, p. 169, pl. 5, figs. 1–5 (complete synonymy).

A cranidium, free cheek, and pygidium are figured from boulder SS-36 which agree with the well-known European species in all details. The cranidium possesses no brim, and the deep arcuate marginal furrow bears the usual row of pits. The anterior margin of the border is rather arcuate. The anterior end of the convex glabella is just slightly swollen and the pattern of the glabella furrows typical for the species. The palpebral lobes are as long as the posterior half of the glabella and are opposite the same.

The free cheek figured is incomplete. The facial suture is not clearly shown by the specimen.

The pygidium possesses ungrooved pleurae, five pairs of spines, and probably four axial segments.

Pustules cover the cranidium, pygidium, and free cheek.

Remarks.—*A. serratus* is known from the upper Tremadocian of Argentina (Harrington, 1938, p. 255) and from strata of the same age in the Shineton shales of Shropshire, England (Stubblefield and Bulman, 1928, p. 137, pl. 4, fig. 7) and from the *Ceratopyge* limestone of Sweden (Størmer, 1920). This is the first reported occurrence of it in North America.

Figured specimens.—Cranidium, CW-209; pygidium, CW-210; free cheek, CW-211; from SS-36.

Family OLENIDAE Burmeister, 1843
Subfamily OLENINAE Kobayashi, 1935

The genera *Beltella* Lake, 1919, *Angelina* Salter, 1859, and *Andesaspis* Kobayashi, 1935, are Oleninae which have a wide geographic distribution in Tremadocian beds. Also belonging in this category are two genera described by Walcott from the Cordilleran region: *Tostonia* from the Secret Canyon shale, Nevada, and *Moxomia* from the Chushina formation, Robson Peak, British Columbia (Walcott, 1925, p. 117, pl. 18, figs. 10–14 and p. 107, pl. 22, figs. 8, 9). Another genus belonging to this group is Ross's *Paenebeltella* (1951, p. 78, pl. 18, figs. 1, 2, 5, 6; pl. 19, fig. 10) from the Garden City limestone of Utah.

These genera are now known from Europe, Acadia, the Marathon region, the Cordillera of North America, and from Argentina. The cranidia differ from those of earlier olenids in their greater convexity, faint glabellar furrows and ocular ridges, reduced and tapered borders, small anteriorly placed eyes, and comparatively narrow fixed cheeks. In addition, the pygidium is unusually small and the thoracic segments (where known) are not prolonged into spines. The following résumé of these genera and comments thereon are not intended to set up a classification or to indicate for certain affinities or synonymies within either genera or species. It is hoped, however, that the assembling of notes, comparisons, and references will aid in future treatment of these widely distributed and probably related genera seemingly confined to geosynclinal deposits of latest Cambrian and Early Ordovician age.

Genus BELTELLA Lake, 1919

Beltella is defined by Lake (1919, p. 102) as having a quadrate or conical, truncate or rounded glabella, with a brim as wide or wider than the border, with two pairs of narrow but obvious furrows, a rather well-impressed occipital furrow, and anterior facial sutures trending slightly inward posteriorly. The thorax has 12 segments and the pygidium is transverse with a large axis, three axial segments, and a non-spinose posterior margin. The known species are:

1. *B. depressa* (Salter), 1859, type species; Lake, 1919, p. 104, and Stubblefield, 1933, pp. 366–368, pl. 34, figs. 1, 9–11. Comparatively thick but well-tapered border, fixed cheeks less than half glabellar basal width but wider than on most other species, rather square truncate glabella. Lower Tremadocian of Wales.
2. *B. bucephala* (Belt) Lake, 1919, p. 106, pl. 12, figs. 11–15. Eyes more anterior than in *B. depressa*. Glabella is narrower and more conical. Middle and upper Lingula Flags, British Upper Cambrian.
3. *B. versimilis* (Salter), Lake, 1919, p. 107, pl. 13, figs. 1–5. Cranidium relatively longer, longer glabella, narrower fixed cheeks and faint occipital furrow. Occurs with both the above species and Lake suggests that perhaps it is the opposite sex of these.
4. *B. spinifera* Lake, 1940, add. to p. 109, 149, pl. 18, figs. 9, 10. Glabella less quadrate than in *B. depressa* narrowing considerably toward front which is broadly rounded. Long occipital spine directed up and back. Lake considers glabellar shape a more important difference from the type species than the presence of the spine. From Shineton shales, Shropshire, England, Tremadocian.
5. *B. solitaria* Westergård, 1922, p. 140, 199, pl. 14, figs. 1, 2. Much closer to *B. depressa* than to *B. latifrons*. Very short brim and anterior eyes which cause broad posterior limbs. The border is thicker than on *B. latifrons*. Sweden, Andrarum, zone of *Parabolina spinulosa* and *Orusia lenticularis*.

6. *B. ulrichi* (Kayser), Harrington, 1938, p. 201, pl. 7, figs. 9, 13–18. Glabella a little longer than wide, elevated and frontally rounded. Border and brim about equal in size; brim somewhat wider than border in some specimens; occipital ring with medial tubercule; fixed cheeks narrow; ocular ridges weak; occipital furrow well impressed. *Kainella* fauna, lower Tremadocian, northern Argentina.
7. *Beltella* (?) sp. Hutchinson, 1952, p. 83, pl. 3, fig. 16. Description indicates no diagnostic specific characters and species is unnamed. The form is described as having anteriorly convergent facial sutures. This plus a row of tiny pits in the marginal furrow suggest that the form belongs in Kobayashi's genus *Andesaspis*. McLeod Brook formation, upper zone, lower Arenigian, Cape Breton Island, Nova Scotia.
8. *B. latifrons* Wilson, n. sp. Close to *B. depressa* in its wider fixed cheeks and less anterior eyes, but differs from other species in its wider brim and narrow border. Upper Tremadocian (Lower Ordovician), basal Marathon formation, West Texas.

BELTELLA LATIFRONS Wilson, n. sp.
Plate 26, figures 2, 4, 5, 7, 10

Cephalon semi-circular, cranidium rather convex, more so longitudinally than transversely; squarish excluding posterior limbs. Glabella short for the genus, square, moderately convex, well defined; occipital ring straight and occipital furrow moderately impressed, two pairs of weak oblique glabellar furrows on most specimens, third anterior pair just visible on largest specimens. Brim wide (four times size of border at axis), moderately convex and unflared laterally; border narrow and tapered strongly; fixed cheeks commonly less than half but more than one-third basal width of glabella; palpebral lobes anterior to mid-point of cranidium, located opposite distal end of middle pair of glabellar furrows, small, round, and extended; posterior limb broad proximally but sharply tapered and deeply furrowed.

Facial suture intramarginal to center in a very oblique course, trending but slightly inward behind anterolateral corners, but posterior to palpebral lobes very obliquely and sharply outward to cut the posterior margin well inside the genal angle.

Free cheek with a well-defined border as wide as border of cranidium at axis and much wider than distal border on cranidium; ocular platform smoothly convex as is brim; genal spine long on some cheeks, short on others.

Outer surface of free cheeks and cranidia covered with a fine mat of punctae.

Pygidium broadly transverse with large moderately convex axis occupying one-third of total width and with a well-defined anterior half ring, two segments and a bluntly rounded terminal; pleural segments deeply grooved by pleural furrows. Border probably present but broken on specimen.

Occurrence.—Coll. 4, 4 mi. SW Marathon.

Types.—Holotype cranidium, CW-281; paratype pygidium, CW-288, and free cheek, CW-286.

Figured specimens.—Cranidia, CW-283, CW-284.

Genus PAENEBELTELLA Ross, 1951

Ross describes a genus, *Paenebeltella*, from the Garden City formation of Utah (1951, p. 78) which resembles *Beltella* except that the anterior facial sutures are not intramarginal and diverge instead of converge posterior to the anterior corners of the cranidium. The glabella is rather more rounded than that of *Beltella* and the glabellar furrows practically absent. The posterior limbs are broader than usual in species assigned to *Beltella;* otherwise the genera are very similar. The pygidia seemingly are exactly alike.

Genus ANGELINA Salter, 1859

The genus *Angelina* is related to *Beltella* but differs from it in having a generally spinose pygidium with more segmentation, generally narrower fixed cheeks, a row of tiny pits in the marginal furrow and a facial suture trending almost straight back from the anterolateral corner of the cranidium. These cranidial features are shared with *Andesaspis* which may thus also be distinguished from *Beltella* (see below).

Angelina is considered to possess an elongate cranidium, very faint or absent glabellar furrows, no ocular ridge, anteriorly

TABLE 4.—RATIOS ON CRANIDIA OF *Beltella* AND *Andesaspis*

Length of cran. in mm.	Frontal area L. / Total L. of cran.	Basal glab. width / L. of glab. and occ. ring	Fixed cheek width / Basal glab. width
Beltella latifrons			
18.0 (approx.)	—	—	.45
16.0 (approx.)	—	.92	.33
14.2	.33	.84	.37
12.3	.32	.95	.50
10.6	.28	.73	.36
10.4 (approx.)	—	.80	.45
10.5	.34	.78	.41
10.4 (approx.)	—	.80	.45
10.2	.33	.90	.36
10.2	.34	.97	.31
10.0	.35	.92	.37
9.0	.30	.83	.40
8.3	.34	.82	.33
7.7	.29	.78	.42
7.5	.33	.88	.41
7.0	.31	.92	.36
4.1	.29	.86	.40
4.1	.29	.86	—
Beltella ulrichi (from Harrington's measurements and photographs)			
8.25	.18	.75	.24
7.5	.21	.82	.27
Beltella depressa (from Lake's photographs)			
12.5	.20	.95	.39
12.0	.23	.94	.40
Andesaspis argentinensis (from coll. 2, 4 mi. SW Marathon)			
10.8	.21	.82	.27
7.3	.18	.75	.24

placed palpebral lobes, and 14 to 15 thoracic segments; on some species the pygidium is not spinose but in all species it is more triangular and less broad than that of *Beltella*.

1. *A. sedgewicki* Salter, 1859, type species; Lake, 1919, p. 112, pl. 13, figs. 7–12, pl. 14, fig. 1. The species possesses all the characteristics of the cranidium described above. The frontal limb ratio is about 0.25 and the fixed cheeks narrow; the palpebral lobe is not in such an anterior position as in other species of the genus. The pygidium is small, semicircular and spinose, containing three axial segments plus a terminal; two pleural segments with drooping spine. Upper Tremadoc.
2. *A. punctolineata* Kobayashi, 1938a, p. 479, pl. 6, fig. 22. Larger eyes than on *A. sedgewicki*. Kobayashi states that it has a "subsquare glabella" but his figure shows actually a very elongate one. The glabella is longer and the fixed cheeks narrower than on *A. steinmanni* (Kayser). *Kainella* fauna, lower Tremadocian, Bolivia.
3. *A. steinmanni* (Kayser), Harrington, 1938, pp. 199–201, pl. 8, figs. 1–7, 11, 12. Harrington gives a synonymy of the species. The glabella is relatively shorter and wider than other species. The pygidium is not spinose but differs from that of *B. ulrichi* with which it is associated in its triangular shape and its narrower axis. The anterior margin of the pygidium is normal to the long axis of the species; on the *B. ulrichi* pygidium it is oblique. The cranidium as a whole is less convex than that of *B. ulrichi*. *Kainella* fauna, lower Tremadocian, Argentina.

It is the writer's opinion that the genus *Corbinia* Walcott, 1925, is probably a synonym of *Angelina* Salter, 1859. The species

C. horatio and *C. valida* are quite similar to *A. punctolineata* Kobayashi, 1938. Walcott's original material needs to be restudied.

Genus ANDESASPIS Kobayashi, 1935

The genus *Andesaspis* Kobayashi (1935, p. 66) was diagnosed as possessing "a convex semi-ovate glabella, obscure glabellar furrows, small anterior eyes close to the glabella, narrow frontal limb and rim . . . longitudinal anterior branch of the facial suture in the cephalon." The cephalon of the genus is quite close to that of *Beltella ulrichi* (Harrington, 1938, p. 204 . . . see tables of ratios in this paper) but differs from that of the type species, *B. depressa*, in its narrower fixed cheeks. The cranidium of *Andesaspis* differs from that of *Angelina* in being less elongate and more convex and in having a shorter brim. The pygidium assigned to *Andesaspis* by Kobayashi is, according to Harrington and Kay (1951, p. 661), actually that of *Pseudokainella lata* (Kobayashi). The true pygidium of *Andesaspis* is unknown. But one species of the genus is described.

ANDESASPIS ARGENTINENSIS
Kobayashi, 1935
Plate 26, figures 3, 6

Andesaspis argentinensis KOBAYASHI, 1935, Japanese Jour. Geol. Geogr., vol. 12, no. 3–4, p. 67, pl. 11, figs. 1, 2 (not figs. 3, 4).
Andesaspis argentinensis Kobayashi, HARRINGTON, 1937, Geol. Mag., vol. 74, p. 111, pl. 7, figs. 8–10.
Andesaspis argentinensis KOBAYASHI, 1937, Proc. Imp. Acad. Tokyo, vol. 13, p. 13. (listed only).
Andesaspis argentinensis Kobayashi, HARRINGTON, 1938, Rev. Mus. Plata, sec. paleont., vol. 1, p. 204, pl. 8, figs. 8–10, 14, 16.
Andesaspis argentinensis Kobayashi, HARRINGTON and KAY, 1951, Jour. Paleontology, vol. 25, p. 661 (pygidium removed).

The specimens from the basal Marathon formation agree well with Kobayashi's description. The occipital ring is directed and thickened posteriorly and bears a small median tubercule. This, the less furrowed glabella, narrower fixed cheeks and brim, and row of tiny pits in the marginal furrow serve to distinguish the cranidium from that of *B. latifrons;* the cranidium differs from *B. ulrichi* only in the lack of convergence of the facial suture between the marginal furrow and palpebral lobe. Specimens are from coll. 2 and coll. 4, 4 mi. SW Marathon.

Figured specimens.—Cranidia, CW-290 (coll. 2) and CW-289 (coll. 4).

Two probably related genera belonging to the Tremadocian olenids occur in strata of the Cordilleran geosyncline. These are *Moxomia* Walcott (1925, p. 107) from the Chushina formation near Robson Peak, British Columbia and *Tostonia* Walcott (1925, p. 117) from the Secret Canyon shale, Eureka district, Nevada. Kobayashi (1936b, pp. 97, 98 and 1935, p. 66) discusses the olenid affinities of these genera and comments on their distinguishing characteristics. Comparison of photographs and descriptions indicates that the forms differ from *Beltella* and *Andesaspis* in their nontapered border, less anterior position of the palpebral lobes and deeper glabellar furrows. Restudy of the material on which the genera were based is needed to compare them with Tremadocian olenids described by Harrington and Kobayashi from South America as well as those from the Marathon formation of West Texas.

Genus TOSTONIA Walcott, 1925
TOSTONIA sp. undet.
Plate 26, figure 4

Pygidium subtriangular with oblique anterior margin. Axis one-third total width, sharply tapered with probably five axial segments and a terminal portion. Pleurae deflexed smoothly but steeply with at least four flat pleural segments on each side, these draped obliquely backward and medially grooved by pleural furrows parallel to interpleural grooves; on anterior portion of each pleural segment two or three tubercules present; pleural segments end in short, blunt, backward curved spines; no border present. Resembles *A. argentinensis* pygidium figured by Harrington (1938, pl. 8, fig. 9). The spine tips are not well developed on the Marathon specimen, possibly because of its small size (immature ?) but in all basic features it closely resembles the pygidium assigned by Walcott to *Tostonia iole* (1925, p. 117, pl. 18, figs. 13, 14).

Some resemblance also exists to the tiny pygidium figured, described, but not named by Shaw (1951, p. 114, pl. 22, fig. 19) from the probably Tremadocian beds of the Gorge formation. However, the entire mar-

gin and wide axis distinguish Shaw's specimen from the Marathon form.

Figured specimen.—Pygidium, CW-285, coll. 4, 4 mi. SW Marathon.

Genus PARABOLINELLA Brögger, 1882
PARABOLINELLA INCERTA (Rasetti), 1945
Plate 26, figures 18–22

Parabolina ? incerta RASETTI, 1945, Jour. Paleontology, vol. 19, p. 471, pl. 61, figs. 16.
Parabolinella incerta (Rasetti), SHAW, 1951, Jour. Paleontology, vol. 25, p. 102.

Cranidium moderately convex, twice as wide as long, not deeply furrowed. Glabella plus occipital ring occupying four-fifths of total length, slightly tapered and rounded anteriorly but retaining typical olenid truncate shape, outlined by distinct but shallow dorsal furrow; three pairs of glabellar furrows: anterior pair faint, posterior pair oblique, sigmoid, and commonly bifurcated; occipital furrow also bifurcated distally, occipital ring with axial node. Border almost straight, tapered far out at ends, very narrow and upturned; brim 3 to 4 times size of border at axis, very slightly flared laterally, striated by typical nerve-like pattern; ocular ridges very distinct and oblique; moderate-sized crescentic palpebral lobes opposite ends of middle pair of glabellar furrows, well forward of glabellar center; fixed cheeks one-third basal width of glabella, slightly downsloping; posterior limb deeply furrowed and sharply tapered laterally. Immature cranidia are known from SS-26.

Facial suture cuts anterior margin well out toward anterolateral corner of cranidium, proceeds straight back to palpebral lobe and behind same out in a sweeping curve at about 45° angle to longitudinal axis.

Free cheek flat with many nerve-like striae on very wide ocular platform, border narrow, genal spine continuous with outer margin of cheek, comparatively short.

The only pygidium which could be assigned to this cranidium by association is not of olenid type and is described under separate heading.

Remarks.—The facial sutures which barely converge toward the palpebral lobes and their sigmoid posterior course makes the species resemble those of *Olenus* s.s. However, the narrow fixed cheeks, oblique ocular ridges, and small anteriorly placed palpebral lobes are those of *Parabolinella*. The species resembles *P. incerta* (Rasetti) strongly. The writer's few specimens show some variation in the size of the brim but little or no other variations exist. Shaw has indicated (1951, p. 102) the possibility of synonymy of *P. punctolineata* Kobayashi and *P. incerta* (Rasetti). However, Kobayashi's species possess a less elevated fixed cheek, thicker rim, a row of punctae in the marginal furrow and less developed ocular ridges than *P. incerta* and the writer doubts the synonymy. The species differs from *P. triarthroides* Harrington in several details (see below) and more radically from *P. evansi* Kobayashi from which it may be distinguished by its narrower fixed cheeks, narrower border and smaller, more anteriorly located palpebral lobes.

Specimens of the species occur in boulders SS-26, SS-27, and BM-2. The other members of the fauna in BM-2 resemble those trilobites of boulder BM-4 (*Aphelaspis* zone age). The only trilobites found in SS-26, and SS-27 with *P. incerta* (Rasetti) are figured on plate 26 (figs. 24, 25) and include a fragmentary cranidium described as *Olenus* cf. *O. truncatus* and an undescribed form much resembling types found in the Franconian of the North American province. Rasetti's *P. incerta* from boulder A-3 of the Lévis is a part of the *Hungaia magnifica* fauna which has long been considered of late Trempealeauan age. However A. R. Palmer (personal communication) reports that a few of the trilobites of the *Hungaia magnifica* fauna occur in the western Cordillera at the level of the *Conaspis* zone so that this fauna may be older than heretofore suspected.

Figured specimens.—Cranidia, CW-216 and CW-216b, free cheek, CW-216c, all on same piece of rock; best cranidium, CW-214; fragmentary cranidium and free cheek, CW-218; all from SS-26.

PARABOLINELLA cf. P. TRIARTHROIDES Harrington, 1938
Plate 27, figure 18

Parabolinella triarthroides HARRINGTON, 1938, Rev. Mus. Plata, n. ser., sec. paleon., vol. 1, no. 4, p. 194, pl. 7, figs. 10, 11, text fig. 9.
Parabolinella triarthroides Harrington, SHAW, 1951, Jour. Paleontology, vol. 25, p. 102, pl. 22, figs. 1–10.

This fragmentary cranidium is placed in *P. triarthroides* with some doubt because of the poor material. The cranidium is typically olenid and the medial position of the palpebral lobes and glabellar shape are those of *Parabolinella;* furthermore a definite frontal area is suggested although the anterior part of the cranidium is missing. The rounded, squarish glabella with two pairs of typically olenid furrows suggests Harrington's species. The glabella is more rounded, less quadrate, the fixed cheeks narrower and more convex, and the posterior limbs broader than in *P. incerta* (Rasetti).

Figured specimen.—Cranidium, CW-208, from SS-36.

PARABOLINELLA EVANSI Kobayashi, 1936
Plate 25, figures 10, 15–17

Olenus sp. RESSER in C. E. Evans, 1933, Brisco-Dogtooth map-area, B. C., Summary Rept. Geol. Survey Canada, 1932, pt. A, II, p. 125.
Parabolinella (?) evansi KOBAYASHI, 1936, Japanese Jour. Geol. Geogr., vol. 13, p. 92, pl. 15, figs. 7–9.
Parabolinella evansi KOBAYASHI, 1938, Japanese Jour. Geol. Geogr., vol. 15, p. 186, pl. 16, figs. 11–15.

The writer's material agrees well with Kobayashi's description when allowance is made for flattening shown by the shaly limestone in which Kobayashi's specimens seem to be preserved. His description is considered satisfactorily diagnostic. The essential features distinguishing the cranidium of the species are: (1) the comparatively thick and arcuate border, (2) the medial position of the palpebral lobes which are large thick crescents and joined to the glabella by thick oblique ocular ridges, (3) the narrower posterior limb than is usual for the genus, (4) an axially long frontal area, and (5) a cylindrical glabella with two well-defined oblique pairs of sigmoid furrows and one faint anterior pair.

The following measurements indicate that on cranidia of normal size the fixed cheeks are a little less than half the basal glabellar width, that the frontal area at the axis is about one-third the total cranidial length, and that the border at the axis is from half to one-third the size of the brim. The glabella is relatively longer and the frontal area shorter in smaller specimens.

The facial suture cuts the anterior margin halfway to axis and trends inward back to anterior end of palpebral lobe; the course posterior to eye trends outward obliquely at an angle of about 60°.

The pygidium is atypical for the genus because it is spinose. Kobayashi mentions only four spines on the posterior margin but his figure shows six. The writer's material shows four; it is probable that the number of spines increases with size of the pygidium. This pygidium (fig. 16, pl. 25) is assigned because it is the commonest tail of comparable size associated with the abundant cranidia of boulder BM-4. However, another large but different type of pygidium in the coquina is described and figured (see

TABLE 5.—CRANIDIAL RATIOS ON 13 SPECIMENS OF *Parabolinella evansi*

	Cran. L. in mm.	Frontal area L. / cran. L.	Basal glab. width / L. glab. and occipital lobe	F. cheek width / Basal glabella width	Axial L. border / Axial L. brim
1	13.4	.32	.77	.49	.43
2	11.2	.33	.75	.43	.37
3	9.5	.30	.81	.42	.55
4	7.5 (approx.)	—	—	.45	.42
5	6.6	.30	.74	.44	.33
6	6.4	.32	.75	.35	.54
7	5.2	.30	.74	.48	.50
8	4.9	.35	.72	.43	.42
9	4.8	.32	.69	.50	.34
10	4.3	.35	.72	.45	.50
11	4.2	.28	.75	.40	.40
12	4.0	.24	.67	.25	.46
13	2.8	.29	.68	.41	.58

below). A meraspid cranidium probably of this species is also figured.

Comparisons.—The closest species to *P. evansi* is *P. occidentalis* Wilson, 1951, which occurs in the Ore Hill limestone of the Gatesburg formation of Pennsylvania between the *Elvinia* fauna and the lowest occurrence of *Taenicephalus shumardi* (*Conaspis* fauna). This species differs from *P. evansi* in having a more convex cranidium, narrower, more convex fixed cheeks, and a more tapered and elevated glabella. Also the pygidial fragment described by the writer as associated with the cranidium of the species indicates a non-spinose pygidium for the Appalachian species. Both species differ from the typical Atlantic province species such as *P. limitis* Brögger, *P. leptoplastorum* and *P. laticauda* Westergård, *P. williamsoni* (Belt), *P. triarthra* (Callaway), and *P. triarthroides* Harrington in their wider border, large medially located palpebral lobes, and larger frontal area. Gunnar Henningsmoen and A. B. Shaw (personal communications) have expressed doubt that *P. occidentalis* belongs to the genus *Parabolinella* because of the above differences. It may be that this species and *P. evansi* form a North American branch of the olenids and should be accorded separate generic or even subfamily rank when the forms are better known.

P. evansi differs from *P.* (?) *punctolineata* Kobayashi, 1936, in lacking the punctae in the marginal furrow, in its larger more medially located eyes, and in possession of an arcuate border.

Kobayashi lists no type specimens for this species but his material consisted of specimens collected by Evans from black limestone north of Mount Jubilee, west side of Columbia River, west of Harrogate (P 6/5). The collection was made by the Canadian Geological Survey (see C. E. Evans, 1933, for what little is known of the stratigraphy). Resser (in Evans, 1933) considered the "*Olenus* beds" of this region to be below the *Housia canadensis* zone of the Goodsir (sub-*Elvinia* zone) but Kobayashi correlated them with the middle Franconian. The writer has not studied this material since at present the collections are in Tokyo.

Occurrence.—In boulder BM-4 with *Aphelaspis* species, *Homagnostus obesus*, and species of *Glyptagnostus* and *Pseudagnostus*.

Figured specimens.—Meraspid cranidium, CW-228; pygidium, CW-229; cranidium, CW-230; free cheek, CW-231.

Pygidium sp. undet. 4
Plate 26, figure 26

No cranidia exist in boulder BM-4 which can be certainly assigned to this pygidium which is transverse in shape, with an axis about one-fourth its total width and two-thirds its length, marked by three axial segments plus a terminal. Pleural platform well defined and bears two segments each with a pleural groove. Border smooth and depressed, comparatively wide and markedly inbent posterior to end of axis. Dimensions: 1.75 cm. wide and 8 mm. long.

Figured specimen.—CW-213 from boulder BM-4.

Pygidium sp. undet. 5
Plate 26, figure 25

This pygidium may belong to the cranidium of either *P. incerta* (Rasetti) or *Olenus* cf. *O. truncatus* (see below). Small and triangular, very convex, axis narrow (one-fourth total width), reaching almost to posterior margin, not much tapered posteriorly, bearing seven segments and a posterior portion. Pleural platforms downsloping, well segmented with faint interpleural grooves; border poorly defined; laterally a tiny spine suggested; a slight inbend of posterior margin present axially.

Occurrence.— Boulder SS-26 with the above mentioned species.

Figured specimen.—CW-215.

Genus OLENUS Dalman, 1827
OLENUS cf. O. TRUNCATUS (Brünnich), 1781
Plate 26, figure 24

Olenus truncatus (Brünnich), WESTERGÅRD, 1922, Sver. Geol. Undersökning, Ser. Ca, no. 18, p. 126, pl. 4, figs. 1–4.

Half of a small convex cranidium is figured from boulder BM-2 (also found in BM-4). This arched cranidium may be distinguished from later olenid derivatives such as *Leptoplastus* and *Eurycare* by the anteriorly arched ocular ridges which are characteristic of *O. truncatus* (Westergård, 1922, pl. 4, fig. 2). It may be that undetermined pygidium 5 found in boulder SS-26 belongs to this cranidium since it resembles those of the earlier olenids more than a *Parabolinella* pygidium.

Figured specimen.—Cranidium, CW-212, from BM-2.

Family ASAPHIDAE Burmeister

No definite species are assigned in this family because the asaphids have been so described that it is advisable to have all parts of a single specimen for adequate identification and description. Numerous asaphid fragments occur in calcarenites in beds transitional between the Dagger Flat and overlying Marathon formation. In the three collections, two types of cranidia, three pygidia, and two different hypostomes are known (disregarding the *Symphysurina*) but not enough material exists from any one locality to enable definite associations of various parts of the species.

Genus ASAPHELLUS Callaway, 1877
ASAPHELLUS sp. undet.
Plate 27, figures 3, 11

The following description is based mainly on the largest sample, that of coll. 3, section 4 mi. SW Marathon in the basal Marathon formation. Parts from the other localities are figured and discussed below.

Cranidium very elongate excluding posterior limbs, very moderately convex, all furrows extremely faint so that little relief exists. Glabella shorter than on any species known but occupying more than three-fourths of cranidial length, almost undefined but anterior end visible under proper lighting and evenly deflexed in a smooth curve in front of midpoint; no real glabellar furrows, but faint depressions exist showing three pairs, occipital furrow almost absent. Frontal area wider than usual for genus, smooth and horizontal; fixed cheeks extremely narrow but palpebral lobes form unusually elevated and extended flaps which are semicircular, relatively small, and medially located; posterior limb large and possesses a wide and distinct furrow.

Facial suture intramarginal, forming the ogive-shaped cranidial front, curving smoothly around anterolateral part of cranidium and proceeding straight back to eye; passing up and encircling eye and trending posterolaterally at about 60° to long axis; curving backward to round off large posterior limb.

Free cheek with relatively small semicircular elevated eye above moderately deflexed, smooth ocular platform with a weakly defined border. Genal spine bluntly tapered, relatively short.

Hypostome (one fragment) much like that of *Asaphellus homfrayi* (Salter) but with blunter, more rounded anterior; posterior border broken on one side but hypostome is seemingly unforked.

Pygidium associated with cranidial fragments in two localities is that assigned to *Trigonocerca* Ross.

Specimens studied.—From coll. 3, 4 mi. SW Marathon: cranidia 30, 17, 12, 4.5, and 1.5 mm. long (associated with eight *Trigonocerca* pygidia); from coll. B, RR rd. 1.1 mi. south: cranidia 24 and 6.5 mm. long (associated with three *Trigonocerca* pygidia).

Figured specimens.—Cranidium, CW-271, 4 mi. SW Marathon; cranidium, CW-272, RR rd. 1.1 mi. south.

Genus TRIGONOCERCA Ross, 1951
TRIGONOCERCA sp. undet.
Plate 27, figures 16, 17, 20

Pygidium with narrow axis which is long and gradually tapered, reaching to border; in longitudinal profile horizontal with ten or eleven segments; pleural lobes slightly deflexed, with elevated anterior pleural border and four to six straight but oblique faint segments each showing faint pleural grooves; pleural segmentation ending abruptly at border which is strongly deflexed, evenly concave, about the same width throughout course, and without a spine.

This pygidium although associated with cranidia of *Asaphellus* resembles closely those assigned by Ross (1951, p. 104, pl. 26, figs. 5–13) to *Trigonocerca* and differs considerably from the pygidium of *A. homfrayi*. None of the Marathon pygidia possesses an axial spine but in *Trigonocerca* this feature is lost in maturity. The writer's specimens are evidently older than the species described by Ross (from his zone H of the Garden City) since they occur in the basal Marathon formation with a Gasconade-Tremadocian fauna. The Marathon species also resembles some axially spinose genera of asaphids described from the South American Tremadocian by Kobayashi (1937) and Harrington (1938). For occurrence in the Marathon see *Asaphellus* discussion.

Figured specimens.—Pygidia, CW-269 and CW-270, 4 mi. SW Marathon, coll. 3.

Genus BELLEFONTIA Ulrich, 1925
BELLEFONTIA sp. undet.
Plate 27, figures 9, 19

A pygidium with the depressed transverse form, narrow, multisegmented axis, wide marginal furrow, and well-defined concave border of a *Bellefontia* species is figured from coll. A, RR rd. 1.1 mi. south. An associated cranidial fragment resembles those of *Bellefontia ? acuminiferentis* Ross, 1951, in its larger palpebral lobes and wide rim. The writer doubts that this species is a true *Bellefontia*. The figured cranidial fragment may belong to a different species of *Asaphellus* than that figured in this paper.

Figured specimens.—Pygidium, CW-277; cranidium, CW-276.

Asaphid pygidium, sp. undet.
Plate 27, figure 21

A pygidium from RR rd. 1.1 mi. south of Alsate Creek, coll. B is figured which somewhat resembles those figured and described by Walcott (1925, p. 104, pl. 23, fig. 16) and Ross (1951, pl. 27, fig. 1). However, it differs from those pygidia of *Leiostegium* in being less convex and in having a narrower but more convex border. The shape is that of *Asaphellus* pygidia but the border is quite different. The axis is well elevated, relatively wide and possesses about eight segments.

Figured specimen.—Pygidium, CW-275, RR rd. 1.1 mi. south, coll. A.

Genus SYMPHYSURINA Ulrich, 1925
SYMPHYSURINA cf. S. WOOSTERI Ulrich, 1925
Plate 27, figures 10, 14

Symphysurina woosteri ULRICH, in Walcott 1925, Smithsonian Misc. Coll., vol. 75, no. 3, p. 115, pl. 21, figs. 1–11.

Three fragmentary cranidia occur with *Beltella latifrons*, n. sp., in coll. 4, 4 mi. SW Marathon. These are close to the type species in the bluntly rounded front and large palpebral lobes, which are a little larger than on *S. woosteri*. A median tubercule is present about on the midwidth line of the glabella. The occipital furrow and posterior part of the dorsal furrow are barely suggested. Glabella faintly keeled. Posterior limbs, pygidium, and free cheek unknown.

Figured specimens.—Cranidia, CW-279 and CW-280, coll. 4, 4 mi. SW Marathon.

Subfamily ASAPHINAE Raymond
Species and genus undet.
Plate 26, figure 9

A typically asaphid forked hypostome is figured from coll. A, RR rd. 1.1 mi. south. Since these beds are of Tremadocian age this is certainly one of the oldest recorded occurrences of asaphids with forked hypostomes. Such hypostomes are also present with *Symphysurina* and *Clelandia* in earliest Ordovician strata of the central Appalachians. The Marathon specimen occurs in a coquina of asaphid fragments, but the only parts large enough to be identified are those assigned above to *Bellefontia* and the agnostid *Geragnostus*.

Figured specimen.—Hypostome, CW-278.

Agnostids figured but undescribed

The great numbers and variety of agnostids present both in the faunas from the boulders and in the collections from the Marathon and Dagger Flat formations present problems of taxonomy too great to be undertaken by the writer at this time. However, because these small forms make up such a large and characteristic part of all the faunas, a few of them are figured.

Kormagnostus, cranidium, CW-312, boulder SS-32, Pl. 24, fig. 8.

Baltagnostus, pygidium, CW-304, boulder SS-31, Pl. 24, fig. 23.

Agnostid sp. undet., pygidium, on rock with CW-258, boulder SS-32, Pl. 24, fig. 14.

Pseudagnostus josephus, pygidium, CW-309, on rock with CW-239, boulder BC-2, Pl. 25, fig. 5; cranidium, CW-311, boulder BC-2, Pl. 25, fig. 22.

Pseudagnostus cyclopyge, pygidium, CW-310a, boulder BM-4, Pl. 25, fig. 19; cranidium, CW-313b, boulder BM-4, Pl. 26, fig. 13.

Pseudagnostus bilobus Shaw, pygidium, CW-298, coll. 4, 4 mi. SW Marathon, Pl. 26, fig. 11.

Homagnostus obesus (Belt), pygidium and cranidium, CW-310, boulder BM-4, Pl. 25, fig. 19; pygidium and cranidium, CW-313a, boulder BM-4, Pl. 26, fig. 23; cranidium, CW-232a, boulder BM-4, Pl. 26, fig. 27.

Geragnostus sp., cranidium, CW-299, coll. A, RR rd. 1.1 mi. south, Pl. 26, fig. 16; pygidium, CW-300, coll. A, RR rd. 1.1 mi. south, Pl. 26, fig. 14.

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POPULATION DYNAMICS—A NEW METHOD IN PALEONTOLOGY

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ABSTRACT—The life table method for study of fossil population dynamics is explained, and its prerequisites discussed. The survivorship of the adult mammoth is presented from original data, and some evolutionary and ecological potentialities of the method are briefly indicated.

INTRODUCTION

Its pioneer days being over, the study of population dynamics is now established as a mature branch of ecology, and its important bearing on the problem of evolution mechanics is becoming increasingly clear. Evidently, in order to study the "survival of the fittest" (which is still an important concept, even if natural selection today is given a wider meaning), we shall need data on the actual survival and mortality in natural populations. This is the field of study of the population dynamicist.

The main contributors to our knowledge of the dynamics of natural populations have been the ornithologists, in whose hands the banding methods have yielded results of great importance. Since the advent of this branch of ecology in the 'thirties, a very impressive mass of information concerning avian populations has been gathered; much of the evidence has recently been marshalled in the important contributions by Deevey (1947), Farner (1952), and Hickey (1952).

One deplorable aspect of specialization in modern science is the arrested spread of ideas between workers in different fields, a case in point being the divergence of paleontology and genetics as contributors to evolutionary theory before their recent conjunction. Similarly it has come about that the ornithologists have well-nigh monopolized the study of population dynamics. Yet an age-structure census of an avian population necessitates a long build-up of banding activities, whereas, for instance, a similar census of some mussel populations may be carried out at little cost. In fact, the present position is somewhat suggestive of the German saying,—warum etwas einfach machen, wenn es auch kompliziert geht?

To the paleontologist this field of study holds great promise. At first sight these problems may seem remote from the average sphere of activity of the student of fossils; it may even seem slightly paradoxical to set out and study the expectation of life of animals that became extinct perhaps millins of years ago. But the days when evolutionary paleontology meant nothing beyond the erecting of family trees and the stating of "laws" and "principles" are definitely over. This is not said in order to criticize such methods, which have indeed led to some of the crowning achievements of this science; but there can be no doubt that paleontologists are now turning their interest to new sorts of facts, and are exploring new methods for the study of fossils.

For the time being, paleoecology is lagging badly, perhaps even to the extent of being hardly scientifically respectable in part; and there is certainly no reason for rejecting a tool developed by the neoecologists, when it is applicable to paleo-data. Now, as a fact, many published paleontological data shed important light on problems of population dynamics, *as they stand;* and more may be had, at comparatively little cost.

These notes are intended as a brief introduction to the subject of paleontological population dynamics; some ways in which raw data suitable for this kind of study may be, and have been gathered, will be discussed, and some problems on which they can be brought to bear will be indicated.

THE LIFE TABLE

As many paleontologists are probably not conversant with the technique and aims of population dynamical study, a brief account may be of value. The basic tool of the worker in this field is the life table. It summarizes information on survivorship, rates of mortality, and expectation of life, within a population. These appear as functions of

age (x) in the table; the headings are: l_x, number of survivors remaining at beginning of each age interval; d_x, number of deaths during interval; q_x, rate of mortality during interval ($=d_x/l_x$); e_x, expectation of life, or mean life time remaining to those who have attained the beginning of the age interval. The l_x column starts with a *cohort* of 1000 or 100 individuals, at a stated initial date, preferably birth or fertilization when feasible; the data under q_x are usually given on a per thousand or per cent basis. The table recording the fate of the cohort, may be used in predicting the destiny of another, similar cohort, which is the use to which such tables are put by the life insurance mathematicians. Some other potentialities of the life table treatment will be outlined in a later paragraph.

Table 1 gives, as an instance, the vital statistics for a fossil mammal population, the Pliocene Chinese gazelle, *Gazella dorcadoides* Schlosser, based on a sample of 79 specimens in the Lagrelius collection, Uppsala (from Kurtén, 1953). The initial date has been set at an age of approximately 1.75 years, since the juveniles are underrepresented in the collection.

The l_x column of the life table may be taken as a basis for a graphic survivorship curve, where number of survivors is plotted against age. The ordinate (frequencies) is then preferably scaled logarithmically, whereby the rates of mortality appear directly from the slope of the curve; changing slope, then, indicates a change in the rate of mortality. For the comparison of populations with widely differing absolute longevities, Pearl and Miner (1935) have developed a most useful device: the graphic representations are reduced to a common scale by expressing age in percentage deviation from the mean longevity of the cohort ($=e_x$ at initial date). This is given under x' in the table. In figure 1, a number of survivorship curves for fossil animals are brought together by this method. Some particulars will be given later on.

For more detailed discussions of the life table treatment, the reader is referred to Pearl (1940) and Deevey (1947).

THE RAW DATA

The main prerequisites for life table treatment of a fossil population are as follows.

(a) The sample should be statistically respectable. This does not preclude the study of samples down to 30–40 individuals, which may give useful indication of the cruder outlines of survivorship within a population, but do not suffice for evaluation of finer shadings.

(b) The age at death of the individuals should be known.

(c) Some estimate should be formed regarding the way in which the sample represents the population: whether it may be biassed in any respect, and whether it should be regarded as comparable to a census of a living population, or to a mortality record.

Of these, (a) need hardly be expounded

TABLE 1.—LIFE TABLE FOR THE LOWER PLIOCENE CHINESE GAZELLE, *Gazella dorcadoides*

Based on 79 specimens, adults only, both sexes combined
From Kurtén (1953)

x Age in years	x' Age as per cent deviation from mean longevity	d_x Number dying in age interval	l_x Number surviving at beginning of interval	$100q_x$ Mortality rate per 100 alive at beginning of interval	e_x Expectation of life, or mean after life time at beginning of interval (years)
1.75	−100	33	100	33	2.1
2.75	−152	24	67	36	2.0
3.75	− 5	10	43	23	1.7
4.75	43	16	33	49	1.1
5.75	90	14	17	82	0.7
6.75	138	3	3	100	0.5

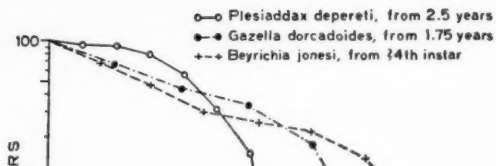

FIG. 1—Adult survivorship curves for the Chinese lower Pliocene mammals *Plesiaddax depereti* and *Gazella dorcadoides* (from Kurtén, 1953), and the Silurian ostracod *Beyrichia jonesi* (data from Spjeldnaes, 1951; time in terms of moults), all based on time-specific analysis, and brought to common scale by expressing age in per cent deviation from expectation of life at initial date. Ordinate (number of survivors) scaled logarithmically; change of slope indicates change in rates of mortality and survival.

upon. Of course homogeneity of sample is desirable, and at times separation of sexes may be of advantage, if possible.

(b), the determination of age at death, is perhaps the most crucial point. In many cases, however, the fossil *per se* permits of an accurate determination. Thus many clams have annual growth rings; on this basis, Winton (1925) has estimated the average life of the Lower Cretaceous *Plicatula dentonensis* at about three years. Annual growth rings are also found in fish scales and otoliths, and in the genital plates of sea-urchins (Moore, 1935). They also occur in the horny sheaths of some bovid horns, which, however, do not often fossilize.

Again, the age at death may be estimated when reliable recent standards are known, as for instance in subfossil horses (Lundholm, 1947). Tooth replacement and wear may give important clues in some proboscideans, the Recent elephant being taken as a standard (see below).

When absolute measures of age are not available, relative measures may be found useful. Thus many invertebrates grow by moults, and some measure of age may be obtained directly as a by-product of growth studies. The survivorship curve for adult *Beyrichia jonesi* (a Silurian ostracod) is based on a body of data by Spjeldnaes (1951); here time is given in terms of moults, no absolute measure of age being available (fig. 1). Again, relative measures of age may be obtained from such data as number of septa in chamber-shelled forms.

If the fossils in themselves do not give sufficient indication of individual age, one possibility may remain. In several cases it has been found that the deposition of fossils was limited, in the main at least, to some particular season of the year. Whenever this happens, and the parturition of the animal in question was seasonal, the remains are bound to form age groups one year apart in age and development. In forms where growth continues throughout life, such samples will exhibit discrete growth series even among the adults; such age groups have been described by Olson and Miller (1951) in Permian amphibians. In mammals, where growth is arrested in maturity, juvenile stages may be distinguished on the basis of growth and tooth replacement (see Loomis, 1910, on *Stenomylus;* Schlosser, 1921, on the *Hipparion* fauna from Veles, Pikermi, and Samos; Matthew, 1924, on *Merychippus*); and finally, if wear of dentition is fast, adult age groups may be delimited by biometric analysis of tooth crown height (Kurtén, 1953, on the Chinese *Hipparion* fauna; see fig. 1).

Given a fossil sample, and the means of dating its members as to age at death, we must turn our interest to the prerequisite, (c). Before entering on an analysis, we must know or be able to form a judgment as to *how* this sample represents the actual population. This is highly dependent on the discretion and discerning of the student.

In some cases it is evident that he has before him a sample of a minor population that has been destroyed simultaneously. This is apparently the case regarding some mass occurrences of fossils, e.g., Pikermi (Abel, 1912); Veles (Schlosser, 1921); the Chinese *Hipparion* fauna (Kurtén, 1953). The sample is then of the *census* type, and mortality is judged from the successive shrinkage in numbers with increasing age. The frequencies within the age groups are thus entered under the heading l_x, and the

other life table functions are computed on this basis. This is *time-specific* analysis.

On the other hand, the data may tend to show that the sample represents a normal mortality record, or the distribution of deaths in the population. If so, the age-group frequencies should be entered under the heading d_x, and the other functions computed accordingly. This is *dynamic* analysis.

It should also be kept in mind that, during the life history of an animal, it may migrate between biotopes, the result being that specimens of different ages may be confined to different types of facies. Such cases will demand great care on the part of the investigator, and it may well be that only segments of the survivorship curve can be obtained. A similar result will obviously ensue when juvenile specimens, as is often the case, are less frequently fossilized than adults. This is the case with the fossil populations of figure 1. When the productivity of the species is known, an estimate may of course be formed regarding the magnitude of juvenile mortality.

FLUCTUATIONS IN POPULATION SIZE

What has been said above obviously pertains to stable populations, in which the losses are exactly replaced by the output of young. Now it is a well-known fact that many populations fluctuate in numbers, some more or less regularly, others irregularly, and others, again, with very long-range trends in increase and decrease (there are no hard and fast boundaries between these three modes). As to the causes for these oscillations, the seasonal fluctuation is obviously correlated with changes in climate, and there is abundant evidence that at least some of the long-range trends are similarly due to climatic change (Kalela 1949, 1950). No final solution to the problem posed by various short-term fluctuations has as yet been found, but Palmgren (1949) has shown that a random variable, probably climatic, in conjunction with autoregression (dependence on last-year population level), may account for some of these.

The fluctuating population, however, introduces an element of bias in the life table. Clearly a time-specific table from the build-up phase of a population cycle will differ from one pertaining to the phase of decline. If, however, the material includes a full cycle or several ones, the resulting survivorship pattern will be a parameter of about the same descriptive value as the mean for a variate.

In neoecology, short-term fluctuations of large amplitude are mainly associated with extreme climatic conditions, and are most common among relatively small animals. Geological and paleontological data, and analogy with present-day conditions, may suffice to indicate whether this complication is likely to arise.

The long-range trends, on the other hand, are not likely to affect the life table very much, and their influence would seem to be overshadowed by random sampling errors except perhaps in extremely large samples.

In spite of these limitations, and those mentioned in the previous paragraph, it is clear that paleontology may give a substantial contribution to this branch of study. The collecting of the raw data may be very simple in principle, and the labor may be almost astonishingly slight when compared to the great apparatus and often decade-long research required by the banding method. As to the handling of the data, the paleontologists will have much to learn from the ornithologists, who have brought their analytic methods to the highest pitch; but it may also be found necessary to develop special techniques for the study of fossil populations.

SURVIVORSHIP IN THE ADULT MAMMOTH

In order to illustrate a case in which some special procedures have to be introduced, the survivorship of the woolly mammoth (*Elephas primigenius*) will be briefly discussed, on the basis of a preliminary survey of a number of specimens in various Finnish and Scandinavian museums.

The sample consists of 11 first molars, 12 second molars, and 44 third molars, in various stages of wear, plus a number of deciduous premolars. On analysis it became apparent that the sample is biassed in favor of permanent molars, since the deciduous teeth are much too scarce to account for the early mortality in the population, the magnitude of which may be estimated on the basis of the productivity in Recent elephants. Hence the juveniles are

not considered, and the age when the first permanent molar was cut is taken as the initial date.

From this stage on the interpretation must proceed on the assumption that the rates of development and living of the woolly mammoth were similar to those of the living elephants. This is certainly a reasonable assumption, since the animals are closely related and about similar in size. In the living forms, the first molar is in function between the approximate ages 6–15 years, the second between 15–30 years, and the third from 30 years to end of potential longevity. This latter datum has been set by Flower (1947) at not much more than half a century. It will therefore be assumed that the oldest specimens on record, represented by some thoroughly used third molars, represent animals that died at about 60 years of age or slightly more.

The subdivisions of these spans of age may be arrived at on the additional assumption that the eroded volume of a tooth is proportional to the time during which this tooth has been in function. Theoretically this might introduce a slight bias, since metabolic rates tend to decelerate with increasing age, but this bias would seem to be completely overshadowed by the virtual impossibility to state the exact percentage of the eroded mass in each case. The results will always remain approximations, no matter how painstaking the analysis.

We now have a body of data giving the age at death of 67 mammoths (fig. 2). (The

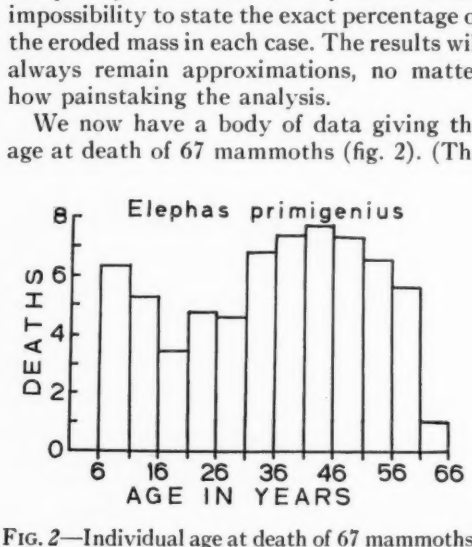

FIG. 2—Individual age at death of 67 mammoths, based on wear of dentition and regrouped in 5-year-intervals, giving frequency distribution of mortality among adult mammoths.

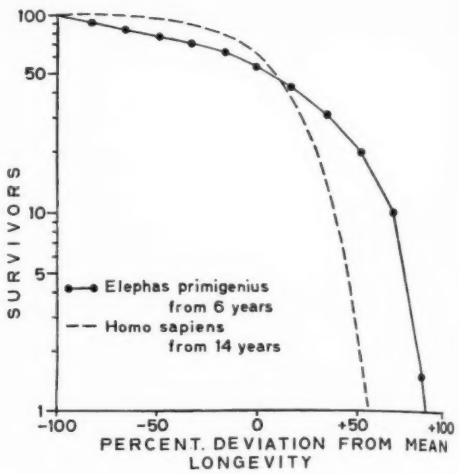

FIG. 3—Survivorship curves for adult mammoths (original data) and adult human males (continental U.S.A., from Allee, et al. 1949), showing basic similarity of pattern.

data were initially grouped in intervals of uneven length, for convenience, and then regrouped in 5-year intervals; hence the fractional values.) It remains to be decided what sort of analysis should be used.

As the peak of the frequency distribution in figure 2 is well removed from its early part it is evident that time-specific analysis is out of question. The older age groups cannot be larger than the younger ones in a stable population, and the sample, of course, does not pertain to the phase of decline in a population cycle. The histogram appears to give the distribution of mortality in the mammoth population, and the analysis is, accordingly, dynamic. The resulting survivorship curve is given in figure 3.

From this curve it may be seen that rates of mortality seem to have been stable and fairly low (some 2 per cent annually) among mammoths in their prime, gradually to increase towards the end of the life span.

PATTERNS OF SURVIVORSHIP

The general pattern of survivorship in adult mammoths would thus be "convex," that is, rates of mortality are increased with age, and the survivorship curve is deflected downwards. The same general pattern is found in adult humans, and the similarity

is clearly brought forth when a human survivorship curve (from subadult age interval 14–15 years) is superposed on the mammoth curve by means of the method of Pearl and Miner (fig. 3). A similar pattern is exemplified by the fossil ovibovine, *Plesiaddax depereti* (fig. 1), and a number of other natural populations (see Deevey, 1947; Kurtén, 1953).

The antithetic type would be the "concave" survivorship, where rates of mortality are decreased with increasing age. This would seem to be a fairly general feature during the early life of a cohort, since juvenile mortality rates commonly exceed adult ones. This type of survivorship should be especially pronounced in, for instance, marine animals with pelagic larvae, and forest trees.

Thirdly, survivorship may remain approximately stable, rates of mortality being about equal regardless of age. This seems to be the case with most adult birds; the corresponding survivorship curves (in arith-log plotting) approach a straight line. *Gazella* and *Beyrichia* (fig. 1) approach this type, but more typical examples of this "diagonal" pattern may be found in extant bird populations. Incidentally, if a worker finds himself in a quandary as to the proper method of analysis, it is well to remember that dynamic and time-specific analysis give closely similar results in the case of diagonal survivorship (and identical in the limiting case).

The descriptive study of such patterns of survival is one of the primary tasks of the population dynamicist. Whenever possible, however, the analysis should proceed further, and patterns of survival should be evaluated as to their ecological and evolutionary implications. Some possibilities may be mentioned; for a more detailed treatment, however, the reader is referred to Kurtén (1953).

Thus the nature of the mortality factors towards the end of the life span of a convex-type cohort may sometimes be inferred. In some cases the main factor may be endogenous senescence (Pearl); but, for instance, regarding *Plesiaddax* and some other mammal populations, it seems clear that the wearing out of the dentition set the limit to potential longevity under natural conditions (exogenous senescence). The bearing of this inference on the problem of progressive hypsodonty is obvious.

Similarly, the factors governing average mortality rates in middle life may be evaluated to some extent from comparisons between related types of animals. Thus the rate of mortality in many terrestrial mammals is inversely related to the gross size of the species, a relation that should be of importance for phyletic growth.

Again, rates of mortality and survival may be studied in connection with rates of development and growth; with changes in environment, as deduced from change in facies; and with evolutionary change. By thus dissecting the life table, the paleontologist may yet be able to give important contributions to the theory of natural selection, despite the denial of some authorities (e.g. Huxley, 1942). This should be heartening to the evolution-minded student of fossils; and perhaps it might help also to promote the common understanding between biological workers on the paleo- and neo-sides that is indispensable for a concerted attack on the problem of organic evolution.

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ARCHAEOCYATHA FROM THE LOWER CAMBRIAN OF INYO COUNTY, CALIFORNIA

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ABSTRACT—A collection of fossils from the Lower Cambrian of Inyo County, California, contains the following genera of Archaeocyatha: *Ajacicyathus*, *Ethmophyllum*, *Pycnoidocyathus*, *Syringocyathus*, *Archaeocyathus*, and *Protopharetra*. Two new species are described: *Archaeocyathus arborensis* and *Syringocyathus inyoensis*.

INTRODUCTION

THROUGH the kindness of Professor J. Wyatt Durham and Professor Joseph H. Peck, Jr., of the University of California at Berkeley the writer was enabled to examine two collections containing Archaeocyatha from Inyo County, California. The collections were designated A-6988 and A-7156 at the Museum of Paleontology at Berkeley. The localities are described as follows: A-6988, Lower Cambrian, Inyo County, California. U.S.G.S. Bishop Quadrangle, Ed. 1913, Silver Peak Group. Collected by Durham and Peck. March 28, 1951. Tan limestones and green shales in the road cuts on the Deep Spring Valley road, running northeast from Zurich. The locality is in Westguard Pass, 11.1 miles from the road junction with U. S. highway 6 at Big Pine, California. A-7156, Lower Cambrian, Inyo County, California. U.S.G.S. Bishop Quadrangle, Ed. 1913. Sec. 8, T8S, R35E. Collected by Peck, Waite, and Tischler, April, 1951. Fossils occur in a tan limestone which weathers red in spots. The locality is just south and east of the Deep Spring Valley road (not over a quarter of a mile off the road) near Cedar Flat, 10 miles east of the junction of the Deep Spring Valley and the Saline Valley roads.

The preservation of the fossils is generally poor, the specimens are mostly barely visible on weathered surfaces. The rock cuts and polishes easily and the polished surfaces show the specimens fairly well. Partial recrystallization and apparently some solution of the fossils after burial obscures much of the necessary detail. In most cases, therefore, only a generic identification is possible.

Even though the collection is small, and generalizations as to the nature of the fauna are hazardous, the impression is gained that the fauna is dominated by the Archaeocyathidae while the Ajacicyathidae, Ethmophyllidae, and Pycnoidocyathidae are in the minority. This is in contrast to the fauna present at Waucoba Canyon, Silver Peak, and northwestern Mexico, where the dominant forms belong to the Ethmophyllidae and Ajacicyathidae. It is also very different from the fauna of British Columbia, where generally the Coscinocyathidae are in the majority. Not enough is known about the vertical and geographical distribution of Archaeocyatha to decide whether such faunal differences are due to their age or are a response to particular environments.

Faunal list from both localities.—*Ajacicyathus nevadensis* (Okulitch), *Ethmophyllum whitneyi* Meek, *Pycnoidocyathus* (*Cambrocyathus*) sp., *Syringocyathus inyoensis* Okulitch, n. sp., *Archaeocyathus atlanticus* Billings, *A.* (*Spirocyathus*) *yavorskii* (Vologdin), *A. arborensis* Okulitch, n. sp., *Archaeocyathus* sp., *Protopharetra dunbari* Okulitch, *Protopharetra* sp., *Archaeopharetra*-type young specimen.

The genus *Syringocyathus* is reported for the first time in North America.

SYSTEMATIC DESCRIPTIONS

Family AJACICYATHIDAE

AJACICYATHUS NEVADENSIS (Okulitch)

Plate 28, figures 6, 7

Ajacicyathus nevadensis (Okulitch), 1943, p. 55, pl. 1, figs. 1, 2, 4.

The species is represented by two small specimens measuring about 2 mm.–4 mm. in diameter. The parieties are spaced relatively far apart. The poor preservation obscures the mural pores. The specimens agree in all particulars with type material from Silver Peak, Nevada.

Locality and horizon.—A-6988, Lower Cambrian.

Family Ethmophyllidae
Ethmophyllum whitneyi Meek, 1886

Ethmophyllum whitneyi Meek, 1886, Am. Jour. Sci., 2nd Ser., vol. 45, pp. 62–64.
Ethmophyllum whitneyi Meek, Okulitch, 1943, p. 64, pl. 3, fig. 15a–c, pl. 4, figs. 1, 3, 4, 8.

A single poorly preserved specimen has been exposed by grinding the rock specimen. Portion of outer wall, intervallum, and the complicated inner wall are visible. The inner wall appears to be vesicular. The appearance of the parieties and inner wall leave no doubt that the specimen is *E. whitneyi*.

Locality and horizon.—A-7156, Lower Cambrian.

Family Syringocnemidae
Syringocyathus inyoensis
Okulitch, n. sp.
Plate 28, figures 4, 5

The genus *Syringocyathus* was established by Vologdin in 1937 on the basis of *S. aspectabilis* to include Syringocnemidae whose intervallum is occupied by prismatic loculi oriented at an acute angle to the central axis. It, therefore, differs from the genus *Syringocnema* in that instead of having radial tubes proceeding from the outer to the inner wall in a horizontal plane, the tubes or loculi are inclined to the axis. The previously known species of *Syringocyathus* were reported only from the Middle Cambrian of Asia. The discovery of the new species extends both the geographical and stratigraphical range of the genus.

The new species is represented by at least six specimens from the A-6988 locality. The preservation is unfortunately poor, but the following characteristics are discernible. The intervallum on a random section, oriented approximately at right angles to the axis of the specimen, appears to be filled by hexagonal and irregular loculi. Oblique sections indicate that the loculi are perforated tubes running obliquely to the axis from the outer to the inner wall. The inner wall is made up of the openings of the tubes and is therefore a coarse net. The outer wall is not shown by any of the available specimens.

It is obvious that such a structure could be produced from a generalized archaeocyathid, such as *Archaeocyathus atlanticus* or a *Protopharetra* by a more orderly development of the dissepiments and taeniae. In fact, in some instances, on random sections it may be difficult to distinguish between these genera, as the differences are not immediately apparent.

The intervallum of the new species is wider than the diameter of the central cavity. The loculi vary in size from 0.5 mm. to 1 mm. in diameter. The laminae enclosing the loculi are not as obviously porous as is the case in the Siberian species. It is at least possible that the previously illustrated (Okulitch, 1943, pl. 6, fig. 6) *Protopharetra* sp. from Silver Peak, Nevada, is a young specimen of *Syringocyathus*.

The description of the new species is based primarily on specimen No. 32961a (paratype) and specimen No. 32961b (holotype). The holotype is about 11 mm. in diameter, with the central cavity only 3 mm. in diameter. The intervallum, at first glance, appears to be filled by numerous taeniae enclosing irregular loculi. However, more careful examination of both specimens reveals that the loculi are elongated chambers inclined to the axis of the specimens. The new species differs from previously described species in the persistently narrow central cavity and lack of obvious pores in the walls of the loculi.

Locality and horizon.—A-6988, Lower Cambrian.

Family Pycnoidocyathidae
Genus Pycnoidocyathus Taylor, 1910
Subgenus Cambrocyathus Okulitch, 1943
Pycnoidocyathus (Cambrocyathus) sp.

The specimens resemble *Pycnoidocyathus ceratodictyoides* (Raymond) from Silver Peak, Nevada, but differ in having less regular parieties. The intervallum coefficient is 1:3, the parietal coefficient is 40:5 or 8.0.

Since the species is represented only by two specimens, both exposed by transverse sections, it is impossible to refer it to any known species with any degree of certainty.

Locality and horizon.—A-7156 Lower Cambrian.

Family ARCHAEOCYATHIDAE

ARCHAEOCYATHUS ATLANTICUS Billings, 1861

Plate 28, figure 9

Archaeocyathus atlanticus BILLINGS, 1861, Geol. Survey, Canada, p. 5.
Archaeocyathus atlanticus Billings, OKULITCH, 1943, p. 68, pl. 5, figs. 1, 2, pl. 18, fig. 18c.

This well-known American species is represented in the collection by several specimens. The species is characterized by its generally cylindrical shape, relatively wide intervallum, and a very coarse network of taeniae in the intervallum.

Locality and horizon.—A-7156 and A-6988, Lower Cambrian.

ARCHAEOCYATHUS (SPIROCYATHUS) YAVORSKII (Vologdin)

Plate 28, figure 8

Spirocyathus yavorskii VOLOGDIN, 1931, pp. 40, 110.
Spirocyathus yavorskii VOLOGDIN, 1940, p. 46.
Archaeocyathus yavorskii (Vologdin), OKULITCH, 1952, p. 31.

This species is very closely related to *A. atlanticus*, from which it differs largely in the more slender and more complicated taeniae. Vologdin included the species in *Spirocyathus*, but since *Spirocyathus* is a synonym of *Archaeocyathus* (Okulitch, 1950), the species *S. yavorskii* should be named *A. yavorskii*. Unfortunately Vologdin using the generic name *Archaeocyathus* in the sense of *Ajacicyathus* (1931 and 1940, p. 53) has described another species as *Archaeocyathus yavorskii* Vologdin (not *Spirocyathus yavorskii*). This second species should properly be named *Ajacicyathus yavorskii* (Vologdin). It is perhaps pertinent to remark that the use of identical specific names for species of related genera can only be regarded as poor practice, which only can lead to confusion.

The species *Archaeocyathus yavorskii* (Vologdin) is represented in the collection by five specimens. This considerably increases its geographic range, since the species was known previously on this continent only from near Caborca, Mexico.

Locality and horizon.—A-7156, Lower Cambrian.

ARCHAEOCYATHUS ARBORENSIS Okulitch, n. sp.

Plate 28, figures 1, 2

The new species differs from all other species of *Archaeocyathus* by producing arborescent forms with several "buds" with distinct oscula arising from the body of the parent. The central cavities of the branches apparently merge into the central cavity of the "trunk." Distally the individuals, on a random cross-section, appear as independent entities, while lower down the buds merge into the body of the parent. The intervallum of *A. arborensis*, n. sp., is filled with curved taeniae, similar to those of *A. atlanticus*. The central cavity is narrow, narrower than in most species of *Archaeocyathus*. In this respect it approaches the narrow central cavity of *Protopharetra*.

The species is based on two specimens. A paratype, No. 32965, Museum of Paleontology, University of California, Berkeley, is from locality A-6988; the holotype, No. C 107 in the paleontological collections of the University of British Columbia, is from Silver Peak, Nevada.

Vologdin has previously described several colonial forms of Archaeocyatha such as: *Densocyathus*, *Sajanocyathus*, and *Pluralicyathus* (*Polycyathus*). In each case the new genus differs from other simple Archaeocyatha only in the ability to reproduce by budding, or by producing two central cavities by infolding of the entire intervallum. Zhuravleva (1950) has quite correctly pointed out that such differences may not be of generic significance. I therefore prefer to retain the new species in the genus *Archaeocyathus*, but indicate its tendency to reproduce by budding by giving it a distinct specific name. Otherwise the species is identical, or very close, to *A. atlanticus*.

Locality and horizon.—A-6988, Lower Cambrian.

Genus PROTOPHARETRA Bornemann, 1886

Protopharetra BORNEMANN, 1886, Nova Acta der K. Leop. Carol, deutschen Akad. Naturf., vol. 51, 1, pp. 27–78.

The genus is represented in the collection by numerous individuals. Of these one was identified as *P. dunbari* Okulitch. The genus *Protopharetra* is of somewhat doubtful validity. Bornemann (1886) regarded it as a

lower vegetative stage from which cups of Archaeocyatha grew. Taylor (1910) restricted the genus to organisms whose intervallum is filled with irregular tissue, which is composed of flattened or cylindrical calcareous fibres, and a narrow central cavity.

It is quite probable that the majority of described *Protopharetra* are young stages of *Archaeocyathus* and related Metacyathida. An even earlier stage of development is represented by the genus *Archaeopharetra* which differs from *Protopharetra* by the absence of even a narrow central cavity. One such specimen is marked "13" in the collection (Pl. 28, fig. 3).

Locality and horizon.—A-6988 and A-7156, Lower Cambrian.

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MANUSCRIPT RECEIVED APRIL 20, 1953

EXPLANATION OF PLATE 28

FIG. *1*—*Archaeocyathus arborensis* Okulitch, n. sp., ×3.5; cross-section, paratype No. 32965, Museum of Paleontology, University of California, Berkeley. Locality A-6988. (p. 295)

2—*Archaeocyathus arborensis* Okulitch, n. sp., ×3. Naturally weathered out specimen. Holotype No. C 107, University of British Columbia. Locality: Silver Peak, Nevada. (p. 295)

3—*Archaeopharetra*-type spitz or young stage of *Archaeocyathus* sp., ×3.5. Cross-section. Locality: A-6988. (p. 296)

4—*Syringocyathus inyoensis* Okulitch, n. sp., ×3, cross-section of a young specimen. Paratype No. 32961a, Museum of Paleontology, University of California, Berkeley. Locality A-6988. (p. 294)

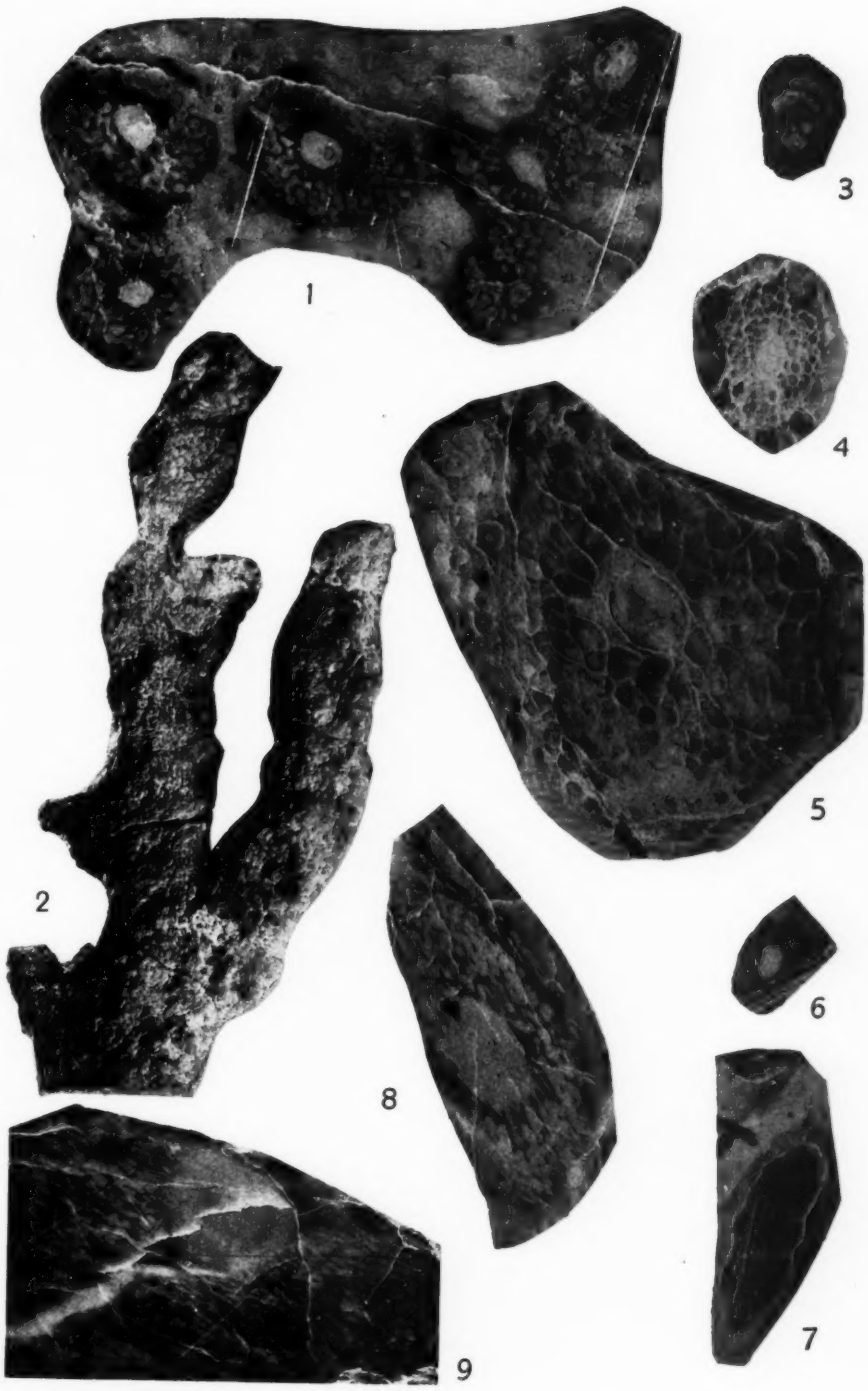
5—*Syringocyathus inyoensis* Okulitch, n. sp., ×4, cross-section of an adult specimen. Holotype No. 32961b, Museum of Paleontology, University of California, Berkeley. Locality A-6988. (p. 294)

6—*Ajacicyathus nevadensis* (Okulitch), ×4. Cross-section of a small specimen. Locality A-6988. (p. 293)

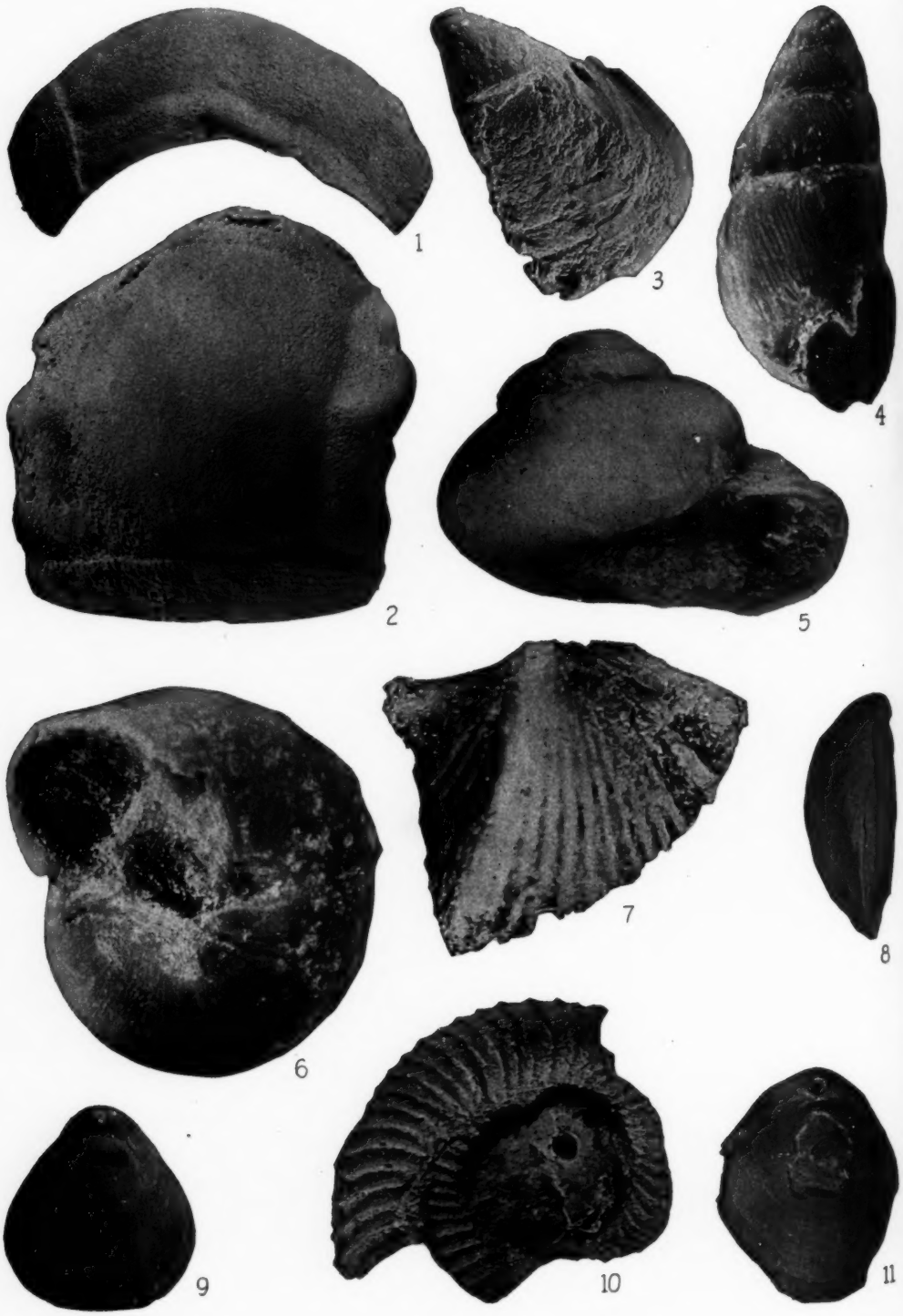
7—*Ajacicyathus nevadensis* (Okulitch), ×4. Cross-section and longitudinal section. Locality A-6988. (p. 293)

8—*Archaeocyathus* (*Spirocyathus*) *yavorskii* (Vologdin), ×4. Locality: A-7156. (p. 295)

9—*Archaeocyathus atlanticus* Billings, ×3. Locality: A-7156. (p. 295)



Okulitch, Archaeocyatha from California



Peck and MacFarland, Whitfield collection types

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 3, PP. 297–309, PL. 29, MAY 1954

WHITFIELD COLLECTION TYPES AT THE UNIVERSITY OF CALIFORNIA[1]

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ABSTRACT—One hundred and ninety-five types and figured specimens of fossil invertebrates from North America contained in a private collection of R. P. Whitfield, which was purchased by the University of California in 1886, are listed in catalogue form. Five of the listed types are figured for the first time and 12 listed by Whitfield as being at the University of California have not been found and are presumed to be lost.

Also listed are 38 types and figured specimens indicated by Whitfield (1899) as being at the University of California but which were never received in Berkeley according to information contained in the catalogue accompanying the collection.

INTRODUCTION

IN 1886, for the sum of $6,290, the University of California purchased from R. P. Whitfield,

> One of the finest collections of fossil mollusca and fossil coal plants extant and numbering in species upwards of 2500, belonging to the following groups: Hamilton, New York chemung, and Rockford, Iowa, chemung groups; Upper Helderberg, Hamilton, Marcellus shale; Waverly, Burlington, St. Louis, and Chester groups; Keokuk limestone and coal fossils, Warsaw coal fossils and Triassic fish, European Liassic, Oolitic, general cretaceous and American Cretaceous, Texan cretaceous, Clairborne, Eocene, Jackson, and Vicksburg groups; large series of fossil plants, Devonian, Lower Carboniferous, and other coal plants; Eocene, Miocene, and a miscellaneous collection of brachiopods showing internal structure; Primordial fossils, Nova Scotian, Devonian plants, and a general assortment of quaternary fossils; geological series, triassic sandstone, foot prints of large reptiles, etc. . . . (Rivers, 1887, p. 56)

Unmentioned by Rivers but included in the shipment were a number of types and figured specimens. The presence of this type material in the collection apparently went unnoticed upon its arrival at Berkeley and insofar as can be determined no notice of the repository, except for Whitfield's list of 1899, has ever been published.

No record of the collection nor of the uses to which it was put are available for the next 50 years although it must have been used for display purposes and, where needed, for class room demonstrations. Curatorial work during this period seems to have been at a minimum or was non-existent.

During the early thirties the first serious attempt to curate the collection was made.

[1] A contribution from the Museum of Paleontology of the University of California.

EXPLANATION OF PLATE 29

FIGS. *1, 2*—*Dikellocephalus eatoni* Whitfield. ×1.3. Side and dorsal views of the cephalon of syntype No. 1213/34336. (p. 307)

3—*Mytilarca percarinata* Whitfield. ×1.3. Beak apparently reconstructed by Whitfield. Holotype No. 1271/34292. (p. 304)

4—*Pupa vermilionensis* Bradley. ×19. Apertural view showing the ornamentation described by Bradley. (The outline of the tooth has been emphasized.) Holotype (?) No. 1931/33006. (p. 306)

5, 6—*Dawsonella meeki* (Bradley). ×19. *5*, apertural view of specimen no. 1932/33007. *6*, umbilical view of specimen no. 1932/33008. Syntypes (?). (p. 304)

7—*Conocardium pulcellum* White and Whitfield. ×15. Left valve. Holotype No. 1119/32436. (p. 303)

8, 9, 11—*Cryptonella calvini* Hall and Whitfield. *8, 9*, side and dorsal views of specimen no. 1067/32455. *11*, dorsal view of specimen no. 1067/32456. Syntypes. (p. 301)

10—*Gyroceras duplicostatum* Whitfield. ×1.3. Latex cast of the original mold. Holotype No. 461/32502. (p. 306)

NOTE: In order to secure maximum detail, conventional lighting procedures were not followed.

ERRATUM: In the title on Plate 29 read "McFarland" for "MacFarland."

In 1933, F. E. Turner, then a research assistant at the Museum, noticed that some of the specimens in the collection had been described and figured. This resulted in a search of the collection and a segregation of specimens which were either types or figured specimens. How complete this search was Turner (personal communication, 1952) does not remember.

Additional efforts to identify and isolate the types and figured specimens of the Whitfield collection were made under the direction of the junior author during the late thirties and early forties and a manuscript was prepared. Subsequent examination has furnished additional types.

Accompanying the collection as purchased was a card catalogue consisting of some 3000 three-by-five cards and a ledger book bearing on the flyleaf the inscription "Catalogue of a collection of fossils owned by R. P. Whitfield, 77th St. and 8th Ave. New York City." Inasmuch as these two catalogues represent the curatorial methods used by Whitfield in taking care of his collection they have been used as final authority to determine whether or not a specimen was originally present in the collection sold to the University.

Whitfield curated his collection in the following manner: Each specimen was given a number which was entered in the ledger book with the identification, location, geologic horizon, and manner in which it was obtained. This number imprinted on a small green or orange (color apparently had no significance) paper ticket was then pasted on the specimen. In addition a three-by-five card was made out bearing the same information present in the ledger book but omitting the manner by which the specimen was obtained. A class number was also present on the card, the use of which is not known. To complete the "bookkeeping" a box label bearing the identification and location was made out. In the case of types or figured specimens the word *type* or *figured* plus the citation, when, known was entered in all three places. The "specimen was [then] marked by a small emerald green paper ticket [diamond] to indicate that [when] a drawing had been made of it for publication" (Whitfield, 1899, p. 140). Guide lines used by the artist are still present on a number of the specimens. There is an exception to the method described above: When more than one individual of the same species was found at the same time and in the same locality, all were marked by the same number and treated as a single unit. This has, in some instances, given rise to the problem of unrecorded paratypes where not only the type, but several other individuals of the same species all bear the same number. Only individuals identified as types or figured specimens are recorded in the present list.

Whitfield (1899) listed 157 types and figured specimens as being present in the University of California collection. In checking this list against the specimens recognized in the collection it was found that a number of inaccuracies were present.

Listed below are the types and figured specimens, whose repository was indicated by Whitfield (1899) to be the University of California, but which, according to the catalogues received with the collection, were never sent to California:

PHYLUM PORIFERA

Cerionites dactyloides Owen
Receptaculites hemisphericus Hall

PHYLUM COELENTERATA

Halysites catenulatus var. *micropora* Whitfield
Omphyma stokesi Edwards and Haime
Omphyma sp.
Strombodes pentagonus (Goldfuss)
Syringopora verticellata (Goldfuss)

PHYLUM ECHINODERMATA

Eucalyptocrinus crassus Hall
Gilbertsocrinus spinigeri Hall

PHYLUM BRACHIOPODA

Hemipronites americanus Whitfield
Meristella laevis Vauxheim
Productus elegans Norwood and Pratten
Productus pileiformis McChesney
Retzia formosa Hall
Rhynchonella hydraulica Whitfield
Rhynchonella neglecta Hall
Spirifera rockymontana Marcou
Spiriferina ziczac Hall
Streptorhynchus crassum Meek and Worthen
Streptorhynchus flabellum Whitfield
Terebratella plicata Say
Terebratula turgida Hall

PHYLUM MOLLUSCA

CLASS PELECYPODA

Cuneamya scapha Hall and Whitfield
Goniophora dubia Hall
Modiolopsis pholadiformis Hall

Modiolopsis truncata Hall
Orthodesma contractum Hall

CLASS GASTROPODA

Bellerophon sublaevis Hall
Naticopsis ziczac Whitfield

CLASS CEPHALOPODA

Cyrtoceras camurum Hall
Gomphoceras sciotense Whitfield
Gyroceras seminodosum Whitfield
Orthoceras annulatum Sowerby
Orthoceras nuntium Hall
Trematoceras ohioense Whitfield

PHYLUM ARTHROPODA

Asaphus homolonotoides Walcott
Asaphus susae Calvin
Eurypterus eriensis Whitfield
Leperditia alta Conrad

Types and figured specimens not listed in Whitfield (1899) which were included in the collection now at the University of California are:

PHYLUM BRACHIOPODA

Meristella belle (Hall)
Trematis millepunctata Hall

PHYLUM ARTHROPODA

Parmithrax? walkeri Whitfield

In the collection as purchased from Whitfield were a number of types and figured specimens of authors other than Whitfield. They are listed in the next column.

PHYLUM BRACHIOPODA

Cyrtia radians Hall
Leiorhynchus robustus Hall and Clarke
Trimerella ohioensis Meek
Triplesia ortoni (Meek)

PHYLUM MOLLUSCA

CLASS PELECYPODA

Actinopteria eximia Hall

CLASS GASTROPODA

Dawsonella meeki (Bradley); [*Anomphalus meeki* Bradley] (Types?)
Hyolithes ligea Hall
Hyolithes principalis Hall
Platyceras crassum Hall (Type?)
Pupa vermilionensis Bradley (Type?)

The types and figured specimens tabulated below, now present at the University of California, were listed by Whitfield in 1899 as being at other institutions or in private collections.

The specimens in the Whitfield collection of types present at the University of California are now identified by a set of numbers similar to the following: 1313/34211. The first number is the original Whitfield collection number, the second is the number assigned to the specimen in the Museum of Paleontology. Additional data, type, age locality, and remarks (if needed) follow. Where the locality listed in the catalog differs from that which has been published,

NAME	LISTED REPOSITORY
PHYLUM PORIFERA	
Receptaculites ohioensis Hall and Whitfield	State Mus., State Univ., Columbus, Ohio
PHYLUM BRACHIOPODA	
Crania carbonaria Whitfield	Prof. Hall's collection
Cryptonella calvini Hall and Whitfield	Am. Mus. Nat. Hist., New York
Dinobolus parvus Whitfield	High School, Whitewater, Wis.
Lingula covingtonensis Hall and Whitfield	Collection of U. P. James, Cincinnati, Ohio
Lingulella stoneana Whitfield	Amer. Mus. Nat. Hist., New York
Rhynchonella? raricosta Whitfield	State Mus., State Univ., Columbus, Ohio
PHYLUM MOLLUSCA	
CLASS PELECYPODA	
Arca quindecimradiata Gabb	State Collection at Trenton, N. J.
Cardium (*Protocardium*) *perelongatum* Whitfield	State Collection at Trenton, N. J.
Conocardium pulcellum White and Whitfield	State Collection at Trenton, N. J.
Gervilliopsis mimia Whitfield	Rutgers College, New Brunswick, N. J.
CLASS GASTROPODA	
Bellerophon alternodosus Whitfield	Columbia Univ., New York
Globiconcha (*Tylostoma*) *curta* Gabb	Acad. Nat. Sci., Philadelphia, Pa.
Holopea obesa Whitfield	State Collection at Madison, Wis.
PHYLUM ARTHROPODA	
Agraulos (*Bathyurus*) *woosteri* Whitfield	State Collection at Madison, Wis.
Conocephalus? (sic) *quadratus* Whitfield	State Collection at Madison, Wis.

the locality used here is the one which is given in the catalog. These changes are noted in the remarks.

In all cases the specimen has been compared directly with the original illustration. Five types are illustrated for the first time.

All species are cited under the original names as given by Whitfield. The age designations here are the ones used by Whitfield in the original publications.

The writers take pleasure in acknowledging their debt to Dr. J. Wyatt Durham for his helpful counsel and criticism. In addition they wish to thank Drs. C. L. Camp, George A. Pettitt, Winifred Goldring, Mr. W. K. Emerson and the many others who gave so freely of their time.

In the following catalogue the specimens are arranged in order of systematic complexity, and secondarily alphabetically by genus and species, and include all types and figured specimens now present at the University of California which were included in the original purchase from R. P. Whitfield. Part B of the catalogue consists of those types and figured specimens listed by Whitfield (1899) as being present at the University of California and listed in the catalogues received with the collection, but which have not been found and must be presumed to have been lost.

PART A: CATALOGUE OF WHITFIELD TYPES PRESENT AT THE UNIVERSITY OF CALIFORNIA

PHYLUM PORIFERA

Receptaculites devonicus Whitfield
Whitfield: 1882a, p. 198; 1890, p. 519, pl. 6, fig. 10
Holotype: 1313/34211, Devonian, Upper Helderberg group; Fisingers' mill on the Scioto River, 11 miles north of Columbus, Ohio.

Receptaculites ohioensis Hall and Whitfield
Hall and Whitfield: 1875, p. 123, pl. 6, fig. 1
Holotype: 175/34212; Silurian, Niagara group; Yellow Springs, Ohio.

PHYLUM COELENTERATA

Cystostylus infundibulus (Whitfield)
Chamberlin: 1877, p. 372 (Check list) [as *Syringopora infundibula*]
Whitfield: 1878, p. 79 [as *Syringopora*]
Chamberlin: 1880, p. 17 (Check list)
Whitfield: 1882, p. 274, pl. 14, fig. 7
Holotype: 645/34350; Silurian, Niagara group, Racine limestone; Harvley's Quarry, Milwaukee, Wis.

Cystostylus typicus Whitfield
Chamberlin: 1877, p. 350 (Check list)
Chamberlin: 1880, p. 18 (Check list)
Whitfield: 1880, p. 64
Whitfield: 1882, p. 274, pl. 14, figs. 8, 9
Holotype: 644/34213; Silurian, Niagara group, Upper Coral beds; Sturgeon Bay, Wis.

Halysites catenulatus Linnaeus
Whitfield: 1882, p. 271, pl. 13, fig. 5
Hypotype: 642/34214; Silurian, Niagara group; Sturgeon Bay, Wis.

Halysites catenulatus Linnaeus var. *labyrinthicus* (Goldfuss)
Whitfield: 1882, p. 272, pl. 13, fig. 7
Hypotype: 643/34215; Silurian, Niagara group; Sturgeon Bay, Wis.

Stylastrea anna Whitfield
Whitfield: 1882a, p. 199; 1890, p. 520, pl. 6, figs. 3?, 5
Syntype: 1257/34216; Devonian, Upper Helderberg limestone; Paulding Co., Ohio.

Stylastrea anna Whitfield
Whitfield: 1882a, p. 199; 1890, p. 520, pl. 6, fig. 4
Syntype: 1257/34217; Devonian, Upper Helderberg limestone; Paulding Co., Ohio.

Stylastrea anna Whitfield
Whitfield: 1882a, p. 199; 1890, p. 520, pl. 6, fig. 4
Syntype? 1257/34218; Devonian, Upper Helderberg limestone; Paulding Co., Ohio.
Remarks: This specimen bearing the green diamond used by Whitfield to mark a type does not resemble the published illustration closely. In view of this, it must be questioned as being one of the types.

Syringopora infundibula (sic) Whitfield
[See *Cystostylus infundibulus*]

Zaphrentis cliffordana Edwards and Haime
Whitfield: 1891, p. 576, pl. 13, fig. 2
Hypotype: 1468/34219; Mississippian, Chester, Maxville limestone; Maxville, Ohio.

Zaphrentis cliffordana Edwards and Haime
Whitfield: 1891, p. 576, pl. 13, fig. 1
Hypotype: 2215/34220; Mississippian, Chester, Maxville limestone; Maxville, Ohio

Zaphrentis cliffordana Edwards and Haime
Whitfield: 1891, p. 576, pl. 13, fig. 3
Hypotype: 2215/34221; Mississippian, Chester, Maxville limestone; Maxville, Ohio.

PHYLUM BRYOZOA

Clathropora clintonensis Hall and Whitfield
Hall and Whitfield: 1875, p. 113, pl. 5, fig. 7
Holotype: 604/34222; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Phaenopora (*Ptilodictya*) *expansa* Hall and Whitfield
Hall and Whitfield: 1875, p. 114, pl. 5, fig. 1
Holotype: 601/34223; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Retepora angulata? Hall
Hall and Whitfield: 1875, p. 111, pl. 5, figs. 2-4
Hypotype: 602/34224; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Rhinopora frondosa Hall and Whitfield
Hall and Whitfield: 1875, p. 112, pl. 5, figs. 8, 9
Holotype: 605/34225; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Stictopora magna Hall and Whitfield
Hall and Whitfield: 1875, p. 112, pl. 5, figs. 5, 6

Holotype: 1129/34226; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

PHYLUM BRACHIOPODA

Athyris subquadrata Hall
Whitfield: 1891, p. 585, pl. 14, figs. 1, 2
Hypotype: 2214/34234; Mississippian, Chester, Maxville limestone; Maxville quarries, Maxville, Ohio.

Athyris subtilita (Hall)
Whitfield: 1891, p. 604, pl. 16, figs. 7–9
Hypotype: 1315/34235; Coal Measures, upper chert band; Widow Bank's farm, Falls Township, Hocking Co., Ohio.

Atrypa nodostriata Hall
Hall and Whitfield: 1875, p. 133, pl. 7, figs. 12–14
Hypotype: 174/34236; Silurian, Niagara group; Yellow Springs, Ohio.

Chonetes reversa Whitfield
Whitfield: 1882a, p. 213; 1890, p. 549, pl. 11, figs. 8, 9
Holotype: 1535/34237; Devonian, Marcellus shale; Smith and Price quarry near Columbus, Ohio.

Chonetes scitula Hall
Whitfield: 1890, p. 548, pl. 11, fig. 10
Hypotype: 1540/34238; Devonian, Marcellus shale; Mr. Meeter's farm 2½ miles south of Dublin, Ohio.
Remarks: Published locality is "from above the Bone bed" at Smith and Price's quarries near Columbus, Ohio.

Crania carbonaria Whitfield
Whitfield: 1882a, p. 229; 1891, p. 599, pl. 15, fig. 11
Syntype: 1328/34240; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.
Remarks: This species bears the same Whitfield number as *Zeacrinus mooresi* Whit.

Crania carbonaria Whitfield
Whitfield: 1882a, p. 229; 1891, p. 599, pl. 15, fig. 12
Syntype: 1328/34239; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.

Crania scabiosa Hall
Hall and Whitfield: 1875, p. 74, pl. 1, fig. 17
Hypotype: 576/34241; Ordovician, Hudson River group; Cincinnati, Ohio.

Cryptonella calvini Hall and Whitfield
Hall and Whitfield: 1873, p. 239
Syntype: 1067/32455; Devonian, Chemung group; Mason City, Iowa.
Remarks: One of two individuals bearing green diamonds and marked *type* on the card accompanying them. Inasmuch as they were never illustrated they are figured here for the first time. Pl. 29, figs. 8, 9.

Cryptonella calvini Hall and Whitfield
Hall and Whitfield: 1873, p. 239
Syntype: 1067/32456; Devonian, Chemung group; Mason City, Iowa.
Remarks: See above. Pl. 29, fig. 11.

Cyrtia radians Hall
Hall and Clarke: 1894, p. 362, pl. 28, figs. 4, 5
Syntype: 680/32451; Silurian, Clinton group; Rochester, New York.
Remarks: The published locality for this species is the Niagara group.

Cyrtia radians Hall and Clarke
Hall and Clarke: 1894, p. 362, pl. 28, fig. 50
Syntype: 680/32452; Silurian, Clinton group; Rochester, New York.
Remarks: See above.

Dinobolus parvus Whitfield
Whitfield: 1882, p. 347, pl. 27, figs. 8–10
Holotype: 1927/34242; Ordovician, Galena limestone; Whitewater, Wis.

Discina lodensis (Hall)
Whitfield: 1890, p. 547, pl. 11, fig. 7
Hypotype: 1285/34243; Devonian, Marcellus shale; Near Columbus, Ohio.
Remarks: The published locality is Dublin, Ohio.

Discina meekana Whitfield
Whitfield: 1882a, p. 228; 1891, p. 598, pl. 15, figs. 1, 2
Syntype: 1340/34244; Coal Measures, Carbon Hill, Hocking Co., Ohio

Discina meekana Whitfield
Whitfield: 1882a, p. 228; 1891, p. 598, pl. 15, fig. 3
Syntype: 1340/34245; Coal Measures; Carbon Hill, Hocking Co., Ohio.

Discina meekana Whitfield
Whitfield: 1891, p. 603, pl. 16, fig. 2
Hypotype: 1520/33005; Coal Measures; Flint Ridge, Ohio.

Discina minuta (Hall)
Whitfield: 1890, p. 547, pl. 11, fig. 5
Hypotype: 1284/34246; Devonian, Marcellus shale; Near Columbus, Ohio.
Remarks: The published locality is Dublin, Ohio.

Discina minuta (Hall)
Whitfield: 1890, p. 547, pl. 11, fig. 6
Hypotype: 1284/34247; Devonian, Marcellus shale; Near Columbus, Ohio.
Remarks: See above.

Leiorhynchus limitaris (Vanuxem)
Whitfield: 1890, p. 550, pl. 11, fig. 11
Hypotype: 1286/34248; Devonian, Marcellus shale, Columbus, Ohio.

Leiorhynchus robustus Hall and Clarke
Hall and Clarke: 1894, pl. 59, figs. 30, 31
Holotype: 1065/34249; Devonian, Chemung group; Steuben Co., New York.

Leptaena barabuensis (Winchell)
Whitfield: 1882, p. 171, pl. 1, fig. 7
Hypotype: 464/34250; Cambrian, Potsdam sandstone; at the north end of Devils Lake near Baraboo, Wis.

Leptaena barabuensis (Winchell)
Whitfield: 1882, p. 171, pl. 1, fig. 6
Hypotype: 464/34252; Cambrian, Potsdam sandstone; at the north end of Devils Lake near Baraboo, Wis.

Leptaena barabuensis (Winchell)
Whitfield: 1882, p. 195, pl. 3, fig. 6
Hypotype: 1205/34251; Ordovician, Lower Magnesian limestone; Eikie's Quarry near Baraboo, Wis.

Lingula covingtonensis Hall and Whitfield
Hall and Whitfield: 1875, p. 67, pl. 1, fig. 1
Plastoholotype: —.12580; Ordovician, Hudson River group; Cincinnati, Ohio.
Remarks: the specimen present in the col-

lection is the gutta percha cast from which fig. 1 was drawn.

Lingula elderi Whitfield
Whitfield: 1880a, p. 472; 1882, p. 345, pl. 27, fig. 2
Paratype: 494/34253; Ordovician, Trenton limestone; Rochester, Minn.

Lingula elderi Whitfield
Whitfield: 1880a, p. 472; 1882, p. 345, pl. 27, fig. 1
Paratype: 494/34254; Ordovician, Trenton limestone; Rochester, Minn.

Lingula elderi Whitfield
Whitfield: 1880a, p. 472, text fig. 1; 1882, p. 345, pl. 27, figs. 3, 4
Syntype: 494/34255; Ordovician, Trenton limestone; Rochester, Minn.

Lingula elderi Whitfield
Whitfield: 1880a, p. 472, text fig. 2; 1882, p. 345, pl. 27, fig. 5
Syntype: 494/34256; Ordovician, Trenton limestone; Rochester, Minn.

Lingula ligea? Hall
Whitfield: 1890, p. 547, pl. 11, figs. 3, 4
Hypotype: 1538/34257; Devonian, Marcellus shale; Smith and Price's Quarries near Columbus, Ohio.

Lingula manni Hall
Whitfield: 1890, p. 546, pl. 11, fig. 1
Hypotype: 1283/34258; Devonian, Marcellus shale; Near Columbus, Ohio.
Remarks: The published locality is Dublia, Ohio.

Lingula manni Hall
Whitfield: 1890, p. 546, pl. 11, fig. 2
Hypotype: 1283/34260; Devonian, Marcellus shale; Near Columbus, Ohio.
Remarks: see above.

Lingulella stoneana Whitfield
Whitfield: 1882, p. 344, pl. 27, figs. 6, 7
Holotype: 1883/34259; Cambrian, Potsdam sand (Mendota beds); Prairie du Sac, Wis.

Meristella bella (Hall)
Whitfield: 1890, p. 510, pl. 5, figs. 9, 10
Hypotype: 1229/34261; Devonian, Lower Helderberg, Onondaga salt; Greenfield, Ohio.

Meristella bella (Hall)
Whitfield: 1890, p. 510, pl. 5, fig. 8
Hypotype: 1229/34262; Devonian, Lower Helderberg, Onondaga salt; Greenfield, Ohio.

Nucleospira rotundata Whitfield
Whitfield: 1882a, p. 194; 1890, p. 511, pl. 5, fig. 11
Syntype: 707/32963; Devonian, Lower Helderberg group; Water lime; Greenfield, Ohio.

Nucleospira rotundata Whitfield
Whitfield: 1882a, p. 194; 1890, p. 511, pl. 5, fig. 12
Syntype: 707/32964; Devonian, Lower Helderberg group; Water lime; Greenfield, Ohio.

Pentamerus oblongus Sowerby
Hall and Whitfield: 1875, p. 137, pl. 7, fig. 9
Hypotype: 1942/34263; Silurian, Niagara limestone; Yellow Springs, Ohio.

Pentamerus pergibbosus Hall and Whitfield
Hall and Whitfield: 1875, p. 139, pl. 7, fig. 10
Holotype: 378/34264; Silurian, Niagara group; Greenville, Darke Co., Ohio.
Remarks: The locality as published is Greenfield.

Pentamerus pes-ovis Whitfield
Whitfield: 1882a, p. 195; 1890, p. 513, pl. 5, fig. 22
Syntype: 1228/34266; Devonian, Lower Helderberg group; Onondaga salt; Greenfield, Ohio.
Remarks: The published locality is Adams Co., Ohio.

Pentamerus pes-ovis Whitfield
Whitfield: 1882a, p. 195; 1890, p. 513, pl. 5, fig. 21
Syntype: 1228/34265; Devonian, Lower Helderberg group; Onondaga salt; Greenfield, Ohio.
Remarks: See above.

Pentamerus pes-ovis Whitfield
Whitfield: 1882a, p. 195; 1890, p. 513, pl. 5, figs. 18–20
Syntype: 1228/34267; Devonian, Lower Helderberg group; Onondaga salt; Greenfield, Ohio.
Remarks: See above.

Rhynchonella pisa Hall and Whitfield
Hall and Whitfield: 1875, p. 135, pl. 7, figs. 18, 19
Syntype: 678/34268; Silurian, Niagara limestone; Danville, Highland Co., Ohio.

Rhynchonella pisa Hall and Whitfield
Hall and Whitfield: 1875, p. 135, pl. 7, fig. 21
Syntype: 678/34269; Silurian, Niagara limestone; Danville, Highland Co., Ohio.

Rhynchonella pisa Hall and Whitfield
Hall and Whitfield: 1875, p. 135, pl. 7, fig. 22
Syntype: 678/34270; Silurian, Niagara limestone; Danville, Highland Co., Ohio.

Rhynchonella? raricosta Whitfield
Whitfield: 1882a, p. 201; 1890, p. 522, pl. 6, fig. 6
Holotype: 1267/34271; Devonian, Upper Helderberg group; Columbus, Ohio.

Spirifera (Martinia) lineata Martin
Whitfield: 1891, p. 603, pl. 16, fig. 6
Hypotype: 1548/34272; Carboniferous, Coal Measures; Railroad at Webb Summit, Hocking Co., Ohio.

Spirifera (Martinia) lineata Martin
Whitfield: 1891, p. 603, pl. 16, figs. 3–5
Hypotype: 1316/34273; Carboniferous, Coal Measures; Widow Bank's farm, Falls Township, Hocking Co., Ohio.

Spirifera maia (Billings)
Whitfield: 1890, p. 549, pl. 11, fig. 14
Hypotype: 1547/34274; Devonian, Marcellus shale; Smith and Price's quarries near Columbus, Ohio.
Remarks: The published locality is Dublin, Ohio.

Strophomena patenta (Hall)
Hall and Whitfield: 1875, p. 115, pl. 5, fig. 10
Hypotype: 612/34275; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Trematis millepunctata Hall
Hall and Whitfield: 1875, p. 70, pl. 1, fig. 7
Hypotype: 575/34276; Ordovician, Hudson River group; Cincinnati, Ohio.

Trimerella ohioensis Meek
Hall and Clarke: 1892, pl. 4A, figs. 8, 9

Hypotype: 1948/34277; Silurian, Niagaran limestone; Highland Co., Ohio.
Remarks: The published locality of this specimen is Ottawa Co., Ohio.

Triplesia ortoni (Meek)
Hall and Clarke: 1892, pl. 11C, fig. 17 [as *Triplecia*]
Hypotype: 179/33201; Silurian, Clinton group; Marl summit of Clinton group, Dayton, Ohio.

PHYLUM ECHINODERMATA

Cyathocrinus somersi Whitfield
Whitfield: 1882a, p. 226; 1891, p. 596, pl. 15, figs. 4, 5
Holotype: 1349/34227; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.

Platycrinus praematurus Hall and Whitfield
Hall and Whitfield: 1875, p. 124, pl. 6, figs. 5, 6
Syntype: 377/34229; Silurian, Niagara group; Greenville, Darke Co., Ohio.

Platycrinus praematurus Hall and Whitfield
Hall and Whitfield: 1875, p. 124, pl. 6, fig. 3
Syntype: 377/34228; Silurian, Niagara group; Greenville, Darke Co., Ohio.

Platycrinus praematurus Hall and Whitfield
Hall and Whitfield: 1875, p. 124, pl. 6, fig. 4
Syntype: 377/34230; Silurian, Niagara group; Greenville, Darke Co., Ohio.

Saccocrinus tennesseensis Troost
Hall and Whitfield: 1875, p. 125, pl. 6, fig. 10
Hypotype: 176/34351; Silurian, Niagara group; Yellow Springs, Ohio.

Zeacrinus mooresi Whitfield
Whitfield: 1882a, p. 227; 1891, p. 597, pl. 15, figs. 8, 9
Syntype: 1328/34231; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.
Remarks: This specimen bears the same Whitfield number as *Crania carbonaria* Whit.

Zeacrinus mooresi Whitfield
Whitfield: 1882a, p. 227; 1891, p. 597, pl. 15, fig. 10
Syntype: 1328/34233; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.
Remarks: See above.

Zeacrinus mooresi Whitfield
Whitfield: 1882a, p. 227; 1891, p. 597, pl. 15, figs. 6, 7
Syntype: 1337/34232; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.

PHYLUM MOLLUSCA

CLASS PELECYPODA

Actinopteria eximia Hall
Hall: 1884, p. 107, pl. 25, fig. 1
Holotype: 760/32697; Devonian, Schoharie grit; Schoharie, New York.

Ambonychia attenuata Hall
Whitfield: 1882, p. 206, pl. 5, fig. 6
Hypotype: 396/34278; Ordovician, Trenton group; Beloit, Wis.

Ambonychia lamellosa Hall
Whitfield: 1882, p. 205, pl. 5, fig. 5
Hypotype: 395/34279; Ordovician, Trenton group; Beloit, Wis.

Ambonychia radiata Hall
Hall and Whitfield: 1875, p. 79, pl. 2, fig. 2
Hypotype: 571/34280; Ordovician, Hudson River group; Waynesville, Ohio.
Remarks: The published locality of the specimen is Cincinnati, Ohio.

Arca quindecimradiata Gabb
Whitfield: 1885, p. 208, pl. 27, fig. 10
Hypotype: 1745/34281; Cretaceous, Upper Marls; New Egypt, New Jersey.

Arca quindecimradiata Gabb
Whitfield: 1885, p. 208, pl. 27, figs. 11–13
Hypotype: 1745/34282; Cretaceous, Upper Marls; New Egypt, New Jersey.

Aviculopecten? equilatera Hall
Whitfield: 1890, p. 551, pl. 11, fig. 16
Hypotype: 1533/34283; Devonian, Marcellus shale; Smith and Price's quarries near Columbus, Ohio.

Aviculopecten interlineatus Meek and Worthen
Whitfield: 1891, p. 604, pl. 16, fig. 10
Hypotype: 1314/34284; Carboniferous, Coal Measures, upper chert band; Widow Bank's farm, Fall Township, Hocking Co., Ohio.

Aviculopecten interlineatus Meek and Worthen
Whitfield: 1891, p. 604, pl. 16, fig. 11
Hypotype: 1314/34285; Carboniferous, Coal Measures, upper chert band; Widow Bank's farm, Fall Township, Hocking Co., Ohio.

Cardium (Protocardium) perelongatum Whitfield
Whitfield: 1885, p. 136, pl. 20, figs. 20, 21
Holotype: 2298/34286; Cretaceous, Lower Green sands; Cream Ridge, New Jersey.
Remarks: The label accompanying this specimen is marked "figured type."

Conocardium pulcellum White and Whitfield
White and Whitfield: 1862, p. 299
Holotype: 1119/32436; Mississippian, Waverly group, Burlington sandstone; Burlington, Iowa.
Remarks: The card accompanying this specimen is marked type. The specimen itself, is glued to a label bearing the notation by Whitfield, "only one." Inasmuch as it was never illustrated it is figured here (pl. 29, fig. 7) for the first time.

Cuneamya miamiensis Hall and Whitfield
Hall and Whitfield: 1875, p. 91, pl. 2, figs. 9, 10
Holotype: 565/34287; Ordovician, Hudson River group; Waynesville, Ohio.

Cypricardites ferrugineum Hall and Whitfield
Hall and Whitfield: 1875, p. 116, pl. 5, fig. 11
Plastoholotype: ——/12581; Silurian, Clinton group; Wilmington, Clinton Co., Ohio.
Remarks: This is the cast from which fig. 11 was drawn.

Cypricardites megambonus Whitfield
Whitfield: 1878, p. 73
Chamberlin: 1880, p. 14 (Check list)
Whitfield: 1882, p. 210, pl. 5, figs. 7, 8
Holotype: 400/34352; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Cypricardites niota Hall
Whitfield: 1882, p. 208, pl. 5, fig. 10
Hypotype: 399/34353; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Cypricardites rotundatus Hall
Whitfield: 1882, p. 208, pl. 5, fig. 11

Hypotype: 397/34354; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Cypricardites ventricosus (Hall)
Whitfield: 1882, p. 209, pl. 5, fig. 9
Hypotype: 398/34288; Ordovician, Trenton group; Hess' quarry, Beloit, Wis.

Gervilliopsis minima Whitfield
Whitfield: 1885, p. 74, pl. 15, fig. 7
Holotype: 1928/34289; Cretaceous, Lower Marls; Freehold, New Jersey

Modiolopsis concentrica Hall and Whitfield
Hall and Whitfield: 1875, p. 86, pl. 2, fig. 18
Holotype: 568/34290; Ordovician, Hudson River group; Waynesville, Ohio.
Remarks: Illustration idealized.

Modiolopsis modiolaris (Conrad)
Hall and Whitfield: 1875, p. 83, pl. 2, fig. 17
Hypotype: 566/34291; Ordovician, Hudson River group; Waynesville, Ohio.

Mytilarca percarinata Whitfield
Whitfield: 1882a, p. 202; 1890, p. 523, pl. 10, figs. 1, 2
Holotype: 1271/34292; Devonian, Upper Helderberg; Dublin, Ohio.
Remarks: Inasmuch as the published figure does not show clearly the characteristics of the specimen; it is re-figured here. Pl. 29, fig. 3.

Orthodesma curvata Hall and Whitfield
Hall and Whitfield: 1875, p. 95, pl. 2, fig. 6
Holotype: 562/34293; Ordovician, Hudson River group; Waynesville, Ohio.

Orthodesma recta Hall and Whitfield
Hall and Whitfield: 1875, p. 94, pl. 2, fig. 7
Syntype: 563/34294; Ordovician, Hudson River group; Waynesville, Ohio.

Orthodesma recta Hall and Whitfield
Hall and Whitfield: 1875, p. 94, pl. 2, fig. 8
Syntype: 563/34295; Ordovician, Hudson River group; Waynesville, Ohio.
Remarks: The illustration is idealized.

Pterinea demissa (Conrad)
Hall and Whitfield: 1875, p. 78, pl. 2, fig. 1
Hypotype: 572/34296; Ordovician, Hudson River group; Cincinnati, Ohio.
Remarks: The illustration is idealized.

Pterinea similis Whitfield
Whitfield: 1882a, p. 214; 1890, p. 551, pl. 11, fig. 15.
Holotype: 1534/34297; Devonian, Marcellus shale; Smith and Price's quarries near Columbus, Ohio.

Tellinomya nasuta Hall
Whitfield: 1882, p. 207, pl. 5, fig. 12
Hypotype: 401/34298; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

CLASS GASTROPODA

Anomphalus meeki Bradley
Bradley: 1872, p. 88, text fig. 2
[See *Dawsonella meeki* (Bradley)]

Bellerophon alternodosus Whitfield
Whitfield: 1882a, p. 225; 1891, p. 593, pl. 14, figs. 17–19
Holotype: 1530/34299; Mississippian, Maxville limestone; Maxville, Ohio.

Bellerophon wisconsensis Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 76
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 223, pl. 6, figs. 15, 16
Holotype: 414/34355; Ordovician, Trenton limestone; Beloit, Wis.

Bucania (*Tremanotus?*) *buelli* Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 76
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 224, pl. 6, figs. 12, 13
Syntype: 407/34356; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Bucania (*Tremanotus?*) *buelli* Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 76
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 224, pl. 6, fig. 14
Syntype: 407/34357; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Clisospira occidentalis Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 75 [as *accidentalis*]
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 222, pl. 5, fig. 21
Holotype: 436/34358; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Cyclonema percarinatum (Hall)
Whitfield: 1882, p. 211, pl. 5, fig. 15
Hypotype: 428/34359; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit Wis.
Remarks: The published locality is Hess' Quarry, Beloit, Wis.

Dawsonella meeki (Bradley)
Bradley: 1872, p. 88, text fig. 2, [as *Anomphalus meeki*]; 1874, p. 151
Syntype?: 1932/33007; Carboniferous, Coal Measures; Little Vermillion River, Vermillion Co., Indiana
Remarks: This is one of two individuals labeled *Dawsonella meeki*, marked by green diamonds, but without other type indication, which are present in the collection. In view of the inadequacy of Bradley's original figure and the lack of any indication that it is a composite, there may be some doubt as to whether or not either of these is the holotype. Figured here. Pl. 29, fig. 5.

Dawsonella meeki (Bradley)
Bradley: 1872, p. 88, Text fig. 2? [as *Anomphalus meeki*]; 1874, p. 151
Syntype?: 1932/33008; Carboniferous, Coal Measures; Little Vermillion River, Vermillion Co., Indiana.
Remarks: See above. Pl. 29, fig. 6.

Euomphalus strongi Whitfield
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 200, pl. 4, figs. 1, 2
Plastoholotype: ——/32487; Ordovician, Lower Magnesian; Richland Co., Wis.

Globiconcha (*Tylostoma*) *curta* Gabb
Whitfield: 1892, p. 160, pl. 19, fig. 26
Hypotype: 1926/32434; Cretaceous; Bell Co., Texas.

Globiconcha (*Tylostoma*) *curta* Gabb
Whitfield: 1892, p. 160, pl. 19, fig. 27
Hypotype: 1926/32435; Cretaceous; Bell Co., Texas.

Holopea obesa Whitfield
Whitfield: 1882, p. 348, pl. 27, fig. 11

Holotype: 1323/34300; Ordovician, Lower Magnesian?; River Falls, Wis.

Hyolithes baconi Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 77
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 225, pl. 6, figs. 10, 11
Syntype: 411/34360; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Hyolithes baconi Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 77
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 225, pl. 6, fig. 9
Syntype: 411/32519; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Hyolithes ligea Hall
Hall: 1877, pl. 27, fig. 13; 1879, p. 195, pl. 32, fig. 14
Hypotype: 772/32858; Devonian, Schoharie grit; Thompson's Lake, Albany Co., New York

Hyolithes principalis Hall
Hall: 1877, pl. 27, figs. 17–19; 1879, p. 196, pl. 32, figs. 17–19, 21
Holotype: 771/32805; Devonian, Schoharie grit; Clarksville, Albany Co., New York.

Loxonema parvulum Whitfield
Whitfield: 1882a, p. 204; 1890, p. 526, pl. 7, fig. 5
Holotype: 1272/32790; Devonian, Upper Helderberg lime; Dublin, Ohio.

Loxonema plicatum Whitfield
Whitfield: 1882a, p. 231; 1891, p. 601, pl. 15, figs. 14, 15
Holotype: 1342/34301; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.

Maclurea bigsbyi Hall
Whitfield: 1882, p. 222, pl. 6, figs. 17, 18
Hypotype: 430/34302; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Macrocheilus priscus Whitfield
Whitfield: 1882a, p. 204; 1890, p. 525, pl. 7, figs. 3, 4
Holotype: 1280/34303; Devonian, Upper Helderberg; Dublin, Ohio.

Macrocheilus regularis (Cox)
Whitfield: 1891, p. 600, pl. 15, fig. 13
Hypotype: 1325/34304; Carboniferous, Coal Measures; Carbon Hill, Hocking Co., Ohio.

Metoptoma barabuensis Whitfield
Whitfield: 1878, p. 60
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 195, pl. 3, figs. 16, 17
Holotype: 1209/34305; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Metoptoma perovalis Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 74
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 211, pl. 5, figs. 13, 14
Holotype: 415/34361; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Metoptoma recurva Whitfield
Whitfield: 1878, p. 61
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 196, pl. 3, figs. 14, 15
Holotype: 1211/34306; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Metoptoma retrorsa Whitfield
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1880, p. 54; 1882, p. 197, pl 3, fig. 18
Holotype: 1210/34307; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Metoptoma similis Whitfield
Whitfield: 1878, p. 61; 1882, p. 196, pl. 3, figs. 12, 13
Holotype: 1212/34308; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Murchisonia gracilis? Hall
Whitfield: 1882, p. 217, pl. 5, fig. 19
Hypotope: 425/34363; Ordovician, Trenton limestone; Railroad quarry near Beloit, Wis.

Murchisonia helicteres Salter
Whitfield: 1882, p. 220, pl. 5, fig. 17
Hypotype: 423/34362; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Murchisonia (*Eunema?*) *pagoda* (Salter)
Whitfield: 1882, p. 218, pl. 5, fig. 20
Hypotype: 1881/34364; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Murchisonia tricarinata Hall
Whitfield: 1882, p. 219, pl. 5, fig. 16
Hypotype: 424/34365; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Murchisonia ventricosa Hall
Whitfield: 1882, p. 218, pl. 5, fig. 18
Hypotype: 422/34366; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.
Remarks: The spire on this specimen has been broken since it was figured.

Naticopsis ortoni Whitfield
Whitfield: 1882a, p. 230; 1891, p. 605, pl. 16, figs. 12, 13, 14?
Holotype: 1317/34309; Carboniferous; Coal Measures; Widow Bank's farm, Fall Township, Hocking Co., Ohio.

Ophileta (*Raphistoma*) *primordialis* (Winchell)
Whitfield: 1882, p. 173, pl. 1, fig. 11
Hypotype: 465/34310: Cambrian, Potsdam sandstone; Devils Lake near Baraboo, Wis.

Ophileta (*Raphistoma*) *primordialis* (Winchell)
Whitfield: 1882, p. 173, pl. 1, fig. 10
Hypotype: 465/34311; Cambrian, Potsdam sandstone; Devils Lake near Baraboo, Wis.

Platyceras crassum Hall
Hall: 1879, pl. 7, fig. 7
Hypotype: 857/32443; Devonian, Upper Helderberg; Clarksville, Albany Co., New York.
Remarks: This specimen lacks the green diamond used to indicate a type, however guide lines used by the artist in making an illustration are present and the notation "Pal. N.Y. vol. V." In view of this, it must be questioned as being the same as figured in Plate 7, figure 7, listed above.

Pleurotomaria subconica Hall
Whitfield: 1882, p. 216, pl. 6, fig. 1
Hypotype: 427/34312; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Pupa vermilionensis Bradley
Bradley: 1872, p. 87, Text fig. 1
Holotype?: 1931/33006; Carboniferous, Coal Measures; Little Vermillion River, Vermillion Co., Indiana.
Remarks: A specimen labeled *Pupa vermilionensis* marked by a green diamond, but without other type indication is present in the collection. In view of the inadequacy of Bradley's original figure there may be some doubt as to whether or not this is the holotype. Figured here. Pl. 29, fig. 4.

Raphistoma lenticularis (Sowerby)
Whitfield: 1882, p. 214, pl. 6, figs. 4, 5
Hypotype: 417/34368; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Raphistoma nasoni (Hall)
Whitfield: 1882, p. 215, pl. 6, figs. 2, 3
Hypotype: 418/34367; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Scaevogyra elevata Whitfield
Whitfield: 1878, p. 62
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 199, pl. 3, fig. 11
Holotype: 1207/34313; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Scaevogyra swezeyi Whitfield
Whitfield: 1878, p. 62
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 198, pl. 3, figs. 7–9
Holotype: 1208/34314; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Trochonema beachi Whitfield
Chamberlin: 1880, p. 14 (Check list)
Whitfield: 1880, p. 55; 1882, p. 213, pl. 6, fig. 6
Holotype: 419/34370; Ordovician, Trenton limestone; Hill above the railroad quarry, Beloit, Wis.

Trochonema beloitense Whitfield
Chamberlin: 1877, p. 299 (Check list)
Whitfield: 1878, p. 74
Chamberlin: 1880, p. 14 (Check list)
Whitfield: 1882, p. 212, pl. 6, figs. 7, 8
Holotype: 421/34369; Hess' quarry, Beloit, Wis.

CLASS SCAPHOPODA

Dentalium martini Whitfield
Whitfield: 1882a, p. 203; 1890, p. 524, pl. 7, fig. 10
Holotype: 1277/34315; Devonian, Upper Helderberg; Dublin, Ohio.

CLASS CEPHALOPODA

Cyrtoceras cretaceum Whitfield
Whitfield: 1882a, p. 209; 1890, p. 531, pl. 8, fig. 3
Syntype: 1278/34316; Devonian, Upper Helderberg lime; Dublin, Ohio.

Cyrtoceras cretaceum Whitfield
Whitfield: 1882a, p. 209; 1890, p. 531, pl. 8, fig. 2
Syntype: 1278/34317; Devonian, Upper Helderberg lime; Dublin, Ohio.

Cyrtoceras planodorsatum Whitfield
Chamberlin: 1880, p. 16 (Check list)
Whitfield: 1880, p. 57 [as *planidorsatum*]; 1882, p. 231, pl. 7, figs. 10–12
Holotype: 450/34318; Ordovician, Trenton limestone; Carpenter's quarry, Beloit, Wis.

Endoceras (*Cameroceras*) *subannulatum* Whitfield
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1880, p. 56; 1882, p. 230, pl. 7, figs. 15, 16
Holotype: 446/34319; Ordovician, Trenton limestone; Below Carpenter's Quarry, Beloit, Wis.
Remarks: The published locality is Hess' Quarry.

Gyroceras columbiense Whitfield
Whitfield: 1882a, p. 210; 1890, p. 532, pl. 10, fig. 8
Holotype: 1279/34320; Devonian, Upper Helderberg lime; Smith and Price's quarry near Columbus, Ohio.

Gyroceras duplicostatum Whitfield
Chamberlin: 1877, p. 325 (Check list)
Whitfield: 1878, p. 78
Chamberlin: 1880, p. 16 (Check list)
Whitfield: 1882, p. 235
Holotype: 461/32502; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.
Remarks: This specimen, an external mold, is accompanied by a card bearing the following notation: "used as type but not figured." Figured here, plate 29, figure 10.

Oncoceras brevicurvatum Whitfield
Chamberlin: 1880, p. 16 (Check list)
Whitfield: 1880, p. 59; 1882, p. 234, pl. 7, fig. 2
Holotype: 457/34321; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Oncoceras mumiaforme Whitfield
Chamberlin: 1880, p. 16 (Check list)
Whitfield: 1880, p. 58; 1882, p. 232, pl. 7, figs. 3, 4
Syntype: 448/34322; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Oncoceras mumiaforme Whitfield
Chamberlin: 1880, p. 16 (Check list)
Whitfield: 1880, p. 58; 1882, p. 232, pl. 7, fig. 5
Syntype: 448/34323; Ordovician, Trenton limestone; Below Carpenter's quarry, Beloit, Wis.

Oncoceras pandion Hall
Whitfield: 1882, p. 233, pl. 7, fig. 6
Hypotype: 460/34371; Ordovician, Trenton limestone; At the top of Carpenter's quarry, Beloit, Wis.

Orthoceras anellum Conrad
Whitfield: 1882, p. 226, pl. 7, fig. 13
Hypotype: 438/34372; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.

Orthoceras (*Actinoceras*) *beloitense* Whitfield
Chamberlin: 1877, p. 325 (Check list) [as *Orthoceras* (*Ormoceras*) *Beloitense* n. sp.]
Whitfield: 1878, p. 77
Chamberlin: 1880, p. 15 (Check list)
Whitfield: 1882, p. 226, pl. 10, fig. 9

Syntype: 444/34324; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.
Remarks: This is one of the two specimens figured by Whitfield: Figure 1 of plate 8 according to Whitfield (1899, p. 180) is in the State Collection formerly at Madison, Wis., part of which has been destroyed by fire.

Orthoceras duseri Hall and Whitfield
Hall and Whitfield: 1875, p. 97, pl. 3, figs. 2–4
Holotype: 1128/34325; Ordovician, Hudson River group; Waynesville, Ohio.

Orthoceras planoconvexum Hall
Whitfield: 1882, p. 228, pl. 7, fig. 14
Hypotype: 443/34373; Ordovician, Trenton limestone; Hess' quarry, Beloit, Wis.
Remarks: The published locality is below Carpenter's quarry, Beloit, Wis.

Orthoceras strix Hall and Whitfield
Hall and Whitfield: 1875, p. 149, pl. 9, fig. 3
Holotype: 1125/34326; Silurian, Niagara limestone; Yellow Springs, Ohio.

Phragmoceras nestor Hall
Whitfield: 1882, p. 301, pl. 19, fig. 3
Hypotype: 686/34327; Silurian, Niagara group, Waukesha limestone; Waukesha, Wis.

PHYLUM ARTHROPODA

Aglaspis eatoni Whitfield
Chamberlin: 1880, p. 10 (Check list)
Whitfield: 1880, p. 52; 1882, p. 192, pl. 10, fig. 11
Holotype: 1218/34379; Cambrian, Potsdam group, Mendota beds; Lodi, Wis.

Agraulos (Bathyurus?) woosteri Whitfield
Whitfield: 1878, p. 56
Chamberlin: 1880, p. 10 (Check list)
Whitfield: 1882, pl. 1, figs. 19, 20
Syntype: 1220/34328; Cambrian, Potsdam sandstone; Eau Claire, Wis.

Agraulos (Bathyurus?) woosteri Whitfield
Whitfield: 1878, p. 56
Chamberlin: 1880, p. 10 (Check list)
Whitfield: 1882, p. 189, pl. 1, fig. 21
Syntype: 1220/32920; Cambrian, Potsdam sandstone; Eau Claire, Wis.

Beyrichia oculifera Hall
Hall: 1872, p. 232, pl. 8, figs. 9, 10
Hall and Whitfield: 1875, p. 103, pl. 4, figs. 9, 10
Holotype: 595/33255; Ordovician, Hudson River group; Cincinnati, Ohio.

Calymene niagarensis Hall
Hall and Whitfield: 1875, p. 153, pl. 6, figs. 14, 15
Hypotype: 688/34330; Silurian, Niagara group; Eaton or Yellow Springs, Ohio.

Conocephalites? quadratus Whitfield
Chamberlin: 1880, p. 10 (Check list)
Whitfield: 1880, p. 47; 1882, p. 180, pl. 1, fig. 16?
Syntype?: 1221/34329; Cambrian, Potsdam sandstone; Eau Claire, Wis.
Remarks: The published figure is so poor that there is some doubt as to whether this specimen is the original of the illustration.

Conocephalites? quadratus Whitfield
Chamberlin: 1880, p. 10 (Check list)
Whitfield: 1880, p. 47; 1882, p. 180, pl 1, fig. 15
Syntype: 1221/32919; Cambrian, Potsdam sandstone; Eau Claire, Wis.

Dicellocephalus barabuensis Whitfield
[See *Dikellocephalus barabuensis*]

Dicellocephalus eatoni Whitfield
[See *Dikellocephalus eatoni*]

Dicellocephalus lodensis Whitfield
[See *Dikellocephalus lodensis*]

Dikellocephalus (sic) *barabuensis* Whitfield
Whitfield: 1878, p. 63 [as *Dicellocephalus*]
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 201, pl. 4, fig. 8
Syntype: 1214/34331; Ordovician, Lower Magnesian; Eikie's quarry, near Baraboo, Wis.

Dikellocephalus (sic) *barabuensis* Whitfield
Whitfield: 1878, p. 63 [as *Dicellocephalus*]
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 201, pl. 4, fig. 9
Syntype: 1214/34334; Ordovician, Lower Magnesian; Eikie's quarry, near Baraboo, Wis.

Dikellocephalus (sic) *barabuensis* Whitfield
Whitfield: 1878, p. 63 [as *Dicellocephalus*]
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 201, pl. 4, figs. 6, 7
Syntype: 1214/34332; Ordovician, Lower Magnesian; Eikie's quarry, near Baraboo, Wis.

Dikellocephalus (sic) *barabuensis* Whitfield
Whitfield: 1878, p. 63 [as *Dicellocephalus*]
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 201, pl. 4, fig. 10
Syntype: 1215/34333; Ordovician, Lower Magnesian; Eikie's quarry, near Baraboo, Wis.

Dikellocephalus (sic) *crassimarginatus* Whitfield
Whitfield: 1882, p. 344, pl. 27, fig. 14
Holotype: 1882/34335, Cambrian, Potsdam sandstone, Mendota beds; Prairie du Sac, Wis.

Dikellocephalus (sic) *eatoni* Whitfield
Whitfield: 1878, p. 65 [as *Dicellocephalus*]
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 202, pl. 4, figs. 11–13
Sytnype?: 1213/34336; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.
Remarks: This specimen does not resemble the illustrations closely. Figured here Pl. 29, figs. 1, 2.

Dikellocephalus (sic) *eatoni* Whitfield
Whitfield: 1878, p. 65 [as *Dicellocephalus*]
Chamberlin: 1875, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 202, pl. 4, figs. 14, 15
Syntype: 1213/34337; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Dikellocephalus (sic) *eatoni* Whitfield
Whitfield: 1878, p. 65 [as *Dicellocephalus*]
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 202, pl. 4, fig. 17
Syntype: 1213/34338; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.
Remarks: Illustration greatly idealized.

Dikellocephalus (sic) *eatoni* Whitfield
Whitfield: 1878, p. 65 [as *Dicellocephalus*]

Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1882, p. 202, pl. 4, fig. 16
Syntype: 1213/34339; Ordovician, Lower Magnesian; Eikie's quarry, near Baraboo, Wis.

Dikellocephalus (sic) *lodensis* Whitfield
Chamberlin: 1880, p. 11 (Check list) [as *Dicellocephalus*]
Whitfield: 1880, p. 51 [as *Dicellocephalus*] 1882, p. 188, pl. 10, fig. 14
Holotype: 1219/34342; Cambrian, Potsdam sandstone, Mendota beds; Lodi, Wis.

Dikellocephalus (sic) *lodensis* Whitfield
Whitfield: 1882, p. 341, pl. 27, fig. 13
Paratype: 1219/34341; Cambrian, Potsdam sandstone, Mendota beds; Prairie du Sac, Wis.

Dikellocephalus (sic) *lodensis* Whitfield
Whitfield: 1882, p. 341, pl. 27, fig. 12
Paratype: 1884/34340; Cambrian, Potsdam sandstone, Mendota beds; Prairie du Sac, Wis.

Encrinurus ornatus Hall and Whitfield
Hall and Whitfield: 1875, p. 154, pl. 6, fig. 16
Holotype: 689/34343; Silurian, Niagara group; Springfield, Ohio.
Remarks: Published locality is Eaton and Yellow Springs, Ohio.

Illaenurus convexus Whitfield
Whitfield: 1878, p. 66
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 203, pl. 4, figs. 3, 4
Syntype: 1216/34344; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Illaenurus convexus Whitfield
Whitfield: 1878, p. 66
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 203, pl. 4, fig. 5
Syntype: 1217/34345; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

Illaenus daytonensis Hall and Whitfield
Hall and Whitfield: 1875, p. 119, pl. 5, fig. 16
Syntype: 606/34346; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Illaenus daytonensis Hall and Whitfield
Hall and Whitfield: 1875, p. 119, pl. 5, fig. 15
Syntype: 606/34347; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

Illaenus ovatus (Conrad)
Whitfield: 1882, p. 238, pl. 5, fig. 1
Hypotype: 432/34375; Ordovician, Trenton limestone; Beloit, Wis.

Illaenus ovatus (Conrad)
Whitfield: 1882, p. 238, pl. 5, fig. 2
Hypotype: 432/34374; Ordovician, Trenton limestone; Beloit, Wis.

Leperditia angulifera Whitfield
Whitfield: 1882a, p. 196; 1890, p. 518, pl. 5, figs. 28, 30
Syntype: 1226/34348; Devonian, Lower Helderberg, Onondaga salt; Greenfield, Ohio.

Leperditia angulifera Whitfield
Whitfield: 1882a, p. 196; 1890, p. 518, pl. 5, figs. 29, 30
Syntype: 1226/32955; Devonian, Lower Helderberg, Onondaga salt; Greenfield, Ohio.

Lichas breviceps Hall
Hall and Whitfield: 1875, p. 156, pl. 6, fig. 17
Hypotype: 607/34349; Silurian, Clinton group; John Brown's quarry near Carlisle, Darke Co., Ohio.
Remarks: Notation on the card accompanying this specimen: "First given as Niagara, Yellow Springs, Ohio. So stands in report."

Paramithrax? walkeri Whitfield
Whitfield: 1883, p. 37, pl. 16, figs. 1a–c, pl. 17, fig. 1
Holotype: 1322/34119; Cretaceous; Near San Antonio, Texas.

PART B: TYPES AND FIGURED SPECIMENS WHICH APPARENTLY ARE LOST

PHYLUM COELENTERATA

Astrocerium venustum Hall
Whitfield: 1882, p. 270, pl. 13, figs. 8–10
Hypotype: 629; Silurian, Niagara group; Beloit, Wis.

Chaetetes fusiformis Whitfield
Whitfield: 1878, p. 70
Chamberlin: 1880, p. 22 (Check list)
Whitfield: 1882, p. 248, pl. 11, figs. 13, 14
Holotype: 1992; Silurian, Hudson River group; Iron Ridge, Wis.
Remarks: Although there are a number of unfigured paratypes? present in the collection, the figured specimen has not been identified.

Stylastrea anna Whitfield
Whitfield: 1882a, p. 199; 1890, p. 520, pl. 6, fig. 1
Syntype: 1257; Devonian, Upper Helderberg limestone; Paulding Co., Ohio.

PHYLUM BRACHIOPODA

Athyris subquadrata Hall
Whitfield: 1891, p. 585, pl. 14, fig. 3
Hypotype: 2214; Mississippian, Chester, Maxville limestone; Maxville quarries, Maxville, Ohio

Nucleospira rotundata Whitfield
Whitfield: 1890, p. 511, pl. 5, figs. 13, 14
Syntype: 707; Devonian, Lower Helderberg group, Water lime; Greenfield, Ohio.

Rhynchonella pisa Hall and Whitfield
Hall and Whitfield: 1875, p. 135, pl. 7, fig. 20
Syntype: 678; Silurian, Niagara limestone; Danville, Highland Co., Ohio.

Schizocrania filosa Hall
Hall and Whitfield: 1875, p. 73, pl. 1, figs. 12–15
Hypotypes: 577; Ordovician, Hudson River group; Cincinnati, Ohio.

PHYLUM MOLLUSCA

CLASS GASTROPODA

Scaevogyra obliqua Whitfield
Whitfield: 1878, p. 63
Chamberlin: 1880, p. 11 (Check list)
Whitfield: 1882, p. 199, pl. 3, fig. 10
Holotype: 1206; Ordovician, Lower Magnesian; Eikie's quarry near Baraboo, Wis.

PHYLUM ARTHROPODA

Beyrichia chambersi Miller
Hall and Whitfield: 1875, p. 104, pl. 4, figs. 11, 12
Hypotypes: 596; Ordovician, Hudson River group; Cincinnati, Ohio.

Beyrichia quadrilirata Hall and Whitfield
Hall and Whitfield: 1875, p. 105, pl. 4, figs. 6, 7
Holotype: 597; Ordovician, Hudson River group; Cincinnati, Ohio.

Illaenus daytonensis Hall and Whitfield
Hall and Whitfield: 1875, p. 119, pl. 5, fig. 14
Syntype: 606; Silurian, Clinton group; Soldier's Home near Dayton, Ohio.

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JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 3, PP. 310–319, PLS. 30–33, 10 TEXT FIGS., MAY 1954

LOWER TURONIAN AMMONITES FROM TEXAS AND MEXICO[1]

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ABSTRACT—*"Hoplitoides" adkinsi*, n. sp., of the family Tissotiidae, subfamily Pseudotissotiinae, and *Spathites chispaensis*, n. gen., n. sp., of the family Vascoceratidae, are described. Other species of *"Hoplitoides"* and of the vascoceratid genera *Fagesia* and *Neoptychites* are described. All specimens are from the Chispa Summit formation (Turonian) of northern Mexico and west Texas. The species of *Spathites* and *"Hoplitoides"* are closely allied to lower Turonian species of North Africa.

INTRODUCTION

THE ammonites discussed in this report include new forms plus previously recorded species from lower Turonian formations of west Texas and northern Mexico. The material has been collected mostly by W. S. Adkins. In spite of the apparent richness of the Turonian faunas of west Texas and northern Mexico the faunas are still very incompletely known. Of the published accounts on Turonian faunas of this area those of Böse (1920, 1928), Adkins (1931, 1933), and Jones (1938) are the most important. The species described here are:

Spathites chispaensis, n. gen., n. sp.
Fagesia texana Adkins
Fagesia haarmanni Böse
Fagesia sp.
Neoptychites cf. *N. xetriformis* Pervinquière
"Hoplitoides" adkinsi, n. sp.
"Hoplitoides" cf. *"H." munieri* Pervinquière

Most of these species are from the Chispa Summit formation of northern Mexico and west Texas and were discussed by Adkins (1931). Adkins' specimens were at the disposal of the writers. New material representing part of the large collections of King and Adkins (1946) from the Chispa Summit formation, Conchos Valley, Chihuahua, Mexico, include numerous beautifully preserved specimens of *Spathites chispaensis* and *"Hoplitoides"* cf. *"H." munieri* Pervinquière.

Spathites was previously recorded by Adkins (1931) as *Pseudotissotia* (?). Adkins' list of the Eagle Ford fauna in 1933 (p. 439) included a notation of three new undescribed genera of the Vascoceratidae in this fauna; these forms include the specimens described here as *Spathites chispaensis*, *"Hoplitoides"* cf. *"H." munieri* Pervinquière and *"Hoplitoides" adkinsi*. *Spathites chispaensis* is closely related to the group of *Vascoceras gongilensis* Wood from the lower Turonian of Nigeria. It represents an early "primitive" development of the Vascoceratidae. Another closely related form is *Nigericeras* Schneegans (1943) from lower Turonian strata of French West Africa. *"Hoplitoides" adkinsi*, n. sp. is allied to the group of *"Hoplitoides" nigeriensis* Wood from lower Turonian of Nigeria and *"Hoplitoides"* cf. *"H." munieri* Pervinquière to the group of *"Hoplitoides" munieri* Pervinquière from lower Turonian strata of Tunisia. None of these species is true *Hoplitoides* and so all should receive separate generic names. The available Texas and Mexican specimens of these species are not sufficiently well preserved or abundant enough to take this step at this time. C. W. Wright informs us that study of a very large collection of Turonian ammonites from Nigeria is now in progress by a French student. This report will include several new genera of Turonian ammonites and one especially for the group of *"Hoplitoides" munieri* and *"H." nigeriensis*. These two groups appear to have gradational forms. These groups likewise are more properly placed in the Pseudotissotiinae of the Tissotiidae rather than the Vascoceratidae.

Fagesia and *Neoptychites* are very rare ammonites in North America. They are discussed again primarily to adequately illustrate the known species from west Texas.

The writers are very grateful to W. S. Adkins, who collected most of the specimens

[1] Published with authorization of the Director, Bureau of Economic Geology, The University of Texas.

discussed in this report, for his advice on many of the problems. Adkins had long ago recognized the taxonomic status of the forms described here. L. B. Kellum of the University of Michigan kindly loaned us the types of *Spathites coahuilaensis* (Jones) and *S. kellyi* (Jones). Mr. C. W. Wright of London, England, has, through personal conversations and correspondence with the senior author, given much advice and help with the broader problems of taxonomy of Cretaceous ammonites. We are pleased to acknowledge our appreciation. The classification used in this report is that of Wright (1952). Finally we wish to thank J. T. Lonsdale, Director of the Bureau of Economic Geology, for permission to study these specimens and to publish this report.

SYSTEMATIC PALEONTOLOGY

Genus SPATHITES Kummel & Decker, n. gen.

Type species.—*Spathites chispaensis* Kummel & Decker, n. sp.

This genus can be briefly diagnosed as follows. Conch involute, compressed, with a subquadrate whorl section. Whorl sides with radial ribs bifurcating from umbilical tubercles, also ribs between primary ones which do not originate in the umbilical tubercles. Besides the umbilical tubercles there are sharp, clavate, double, ventrolateral tubercles. The tuberculation is confined to the early volutions. The adoral part of the phragmocone and the body chamber have no tuberculation and only weak folds. The suture has two irregularly denticulated lateral lobes and three saddles.

Spathites includes those specimens described by Adkins (1931) and Jones (1938) as *Pseudotissotia* (?) from strata of Turonian age in west Texas and northern Mexico. This new genus is most closely related to the group of *Vascoceras gongilensis* Wood (1911) from lower Turonian strata of Nigeria. It differs from that species in having no keel or row of siphonal tubercles at any stage, in its sharp, clavate, double, ventrolateral tubercles instead of single, round and blunt nodes and in the stronger ribs on the early whorls. *Nigericeras* Schneegans (1943) is also similar to *Spathites* but this genus has prominent siphonal tubercles on the early volutions. The ontogenetic development of the conch in these two genera is remarkably similar. Both *Nigericeras* and *Spathites* appear to be early "primitive" vasoceratids retaining a number of ancestral acanthoceratid characters (C. W. Wright, personal communication).

The generic name *Spathites* was suggested by W. S. Adkins and is for L. F. Spath of London, England.

SPATHITES CHISPAENSIS Kummel & Decker, n. sp.

Plate 30, figures 1, 2; plate 31, figures 1–15; text figure 1

Pseudotissotia (?) n. sp. ADKINS, 1931, Univ. Texas Bull. 3101, p. 58, pl. 2, fig. 5; pl. 4, figs. 3, 6.

This species is represented by numerous complete specimens and several fragments. All stages are present from the protoconch to an adult specimen 125 mm. in diameter. Most of the specimens are very well preserved internal molds.

A marked change in development is shown in the ontogeny of the conch. The protoconch is longest transverse to the axis of coiling. The first volution of the conch does not enclose the protoconch, as the elongated ends are still exposed. At a diameter of 5 mm. the conch is smooth, the ventral region is arched and very low ribs are present which trend adorally. At a diameter of 8 mm. the whorl section is compressed, venter flattened and the lateral ribs are enlarged on the ventrolateral area (pl. 31, figs. 7, 8, 9). Umbilical tubercles appear at this stage also. When the conch is 16 mm. in diameter the whorl section is subtrapezoidal with a flattened venter and flattened converging whorl sides (pl. 31, figs. 13, 14, 15). The umbilical shoulders are sharply rounded and the umbilical wall steep and convex. There are prominent umbilical tubercles from which ribs radiate. The ribs are not conspicuous on the whorl sides and there are weak ribs intercalated between those originating in the umbilical tubercles which join sharp, clavate, double, ventrolateral tubercles. At a diameter of approximately 40 mm. the conch is nearly devoid of most of its sculpture. The umbilical and ventrolateral tubercles, and the lateral ribs disappear. The ventral shoulder becomes angular. The ven-

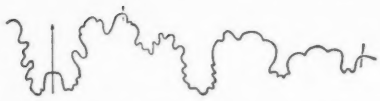


FIG. 1.—*Spathites chispaensis*, n. sp. Diagrammatic representation of the external suture of an unfigured paratype at a diameter of about 70 mm., slightly less than ×1.

ter is flattened, broad, and with transverse ridges (pl. 31, figs. 10, 11, 12). The whorl sides are broadly convex and smooth. The ventral shoulders are angular from a diameter of 45 mm. to a diameter of approximately 80 mm., when they become rounded. The umbilical shoulders are fairly sharply rounded at a diameter of 40 mm. and become less sharply rounded as the diameter of the conch increases.

The body chambers studied are not complete but seem to include about two-thirds of a volution. The whorl section is broad, flat and quadrate with broadly convex flanks, well rounded ventral shoulders, and steeply rounded umbilical shoulders. On the largest specimen, 125 mm. in diameter, the change of the ventral shoulder from angularity to roundness occurs about two-thirds of a volution from the most adoral part of the conch. The transverse ridges on the venter are present approximately to the aperture. These ridges are connected by concave surfaces and are a continuation of the earlier similar ridges on the phragmocone. No actual aperture is present on any of the specimens. All of the larger specimens have a broad shallow lateral constriction at the most adoral part of the conch.

The suture is characterized by narrow lobes and broad saddles. The ventral lobe is long and with blunt denticulations on the sides. It occupies about the central third of the flattened venter. The first lateral saddle is very broad with two or three prominent lobules. The largest lobule is usually just dorsad of the ventral shoulder. The first lateral lobe is shorter than the ventral lobe and irregularly subdivided. The second and third lateral saddles are also broad and with one or more conspicuous lobules. The second lateral lobe is narrow and short. There is a small lobe on the umbilical shoulder.

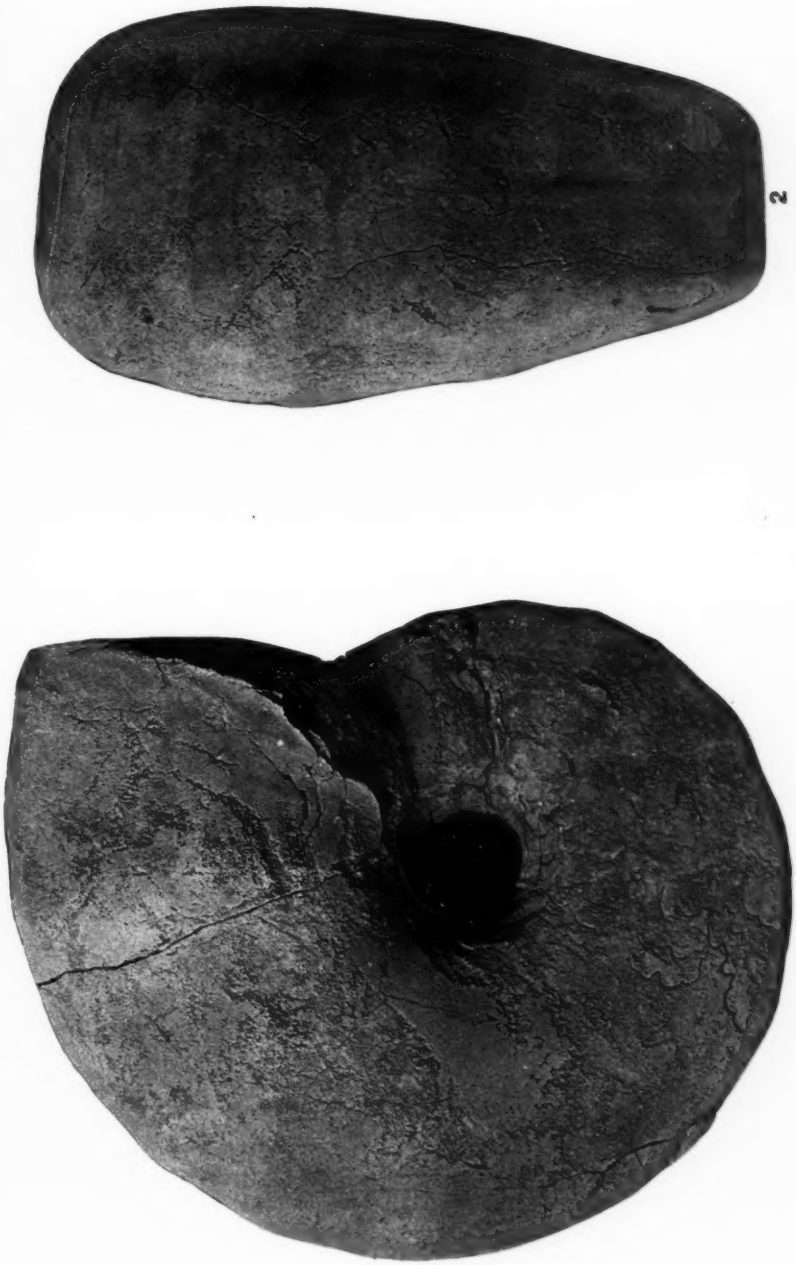
Remarks.—The only other species assigned to this new genus are *Spathites coahuilaensis* (Jones) and *Spathites kellyi* (Jones). The exact horizon and locality of *S. coahuilaensis* is not known. It is very similar to *S. chispaensis* and may be conspecific. The holotype and five paratypes of *Spathites kellyi* are available for study. The specimens are from members 2 and 3, Indidura formation, north of Tanque Toribio, Sierra de Santa Ana, Coahuila, Mexico (Jones, 1938, p. 124). All of the specimens are in a very poor state of preservation making it almost impossible to ascertain their specific affinities; however, the generic characters are sufficiently distinct to make assignment to *Spathites* with certainty. One of the Jones paratypes (1938, pl. 8, fig. 3; Univ. of Mich. No. 16824) has a compressed conch with a narrow tabulate and bicarinate venter. This specimen shows very close similarities with the group of "*Hoplitoides*" *munieri* Pervinquière and is not a *Spathites*. However, its poor preservation prevents anything more than mere speculation as to its affinities. The species of *Nigericeras* described by Schneegans (1943) from French West Africa are generally more evolute than the species of *Spathites* recorded here. However, the ontogeny of the conch, general character of the sculpture, and the suture point to a close relationship between *Spathites* and *Nigericeras*.

Types.—Bureau of Economic Geology, University of Texas, Austin, Texas.

Occurrence.—Chispa Summit formation—(1) Placer de Guadalupe district, Sabaco (San José de Cocahuatál), on the west bank of Conchos River south of Placer de Guadalupe. Turonian basin. Locality 17256, King and Adkins (1946, pl. 4). (2) El Álamo ranch on the north bank of the Conchos River, west of Ojinaga and northeast of Cuchillo Parado. Locality 17255, King and Adkins (1946, pl. 4). (3) U. S. G. S. Loc. 13672, Conchos River, near Cuchillo Parado, Chihuahua, Mexico. (4) Jeff Davis County,

EXPLANATION OF PLATE 30

FIGS. 1, 2—*Spathites chispaensis* Kummel & Decker, n. sp. Lateral and ventral views of the holotype from Placer de Guadalupe district, Sabasco, Mexico, ×1. (p. 311)



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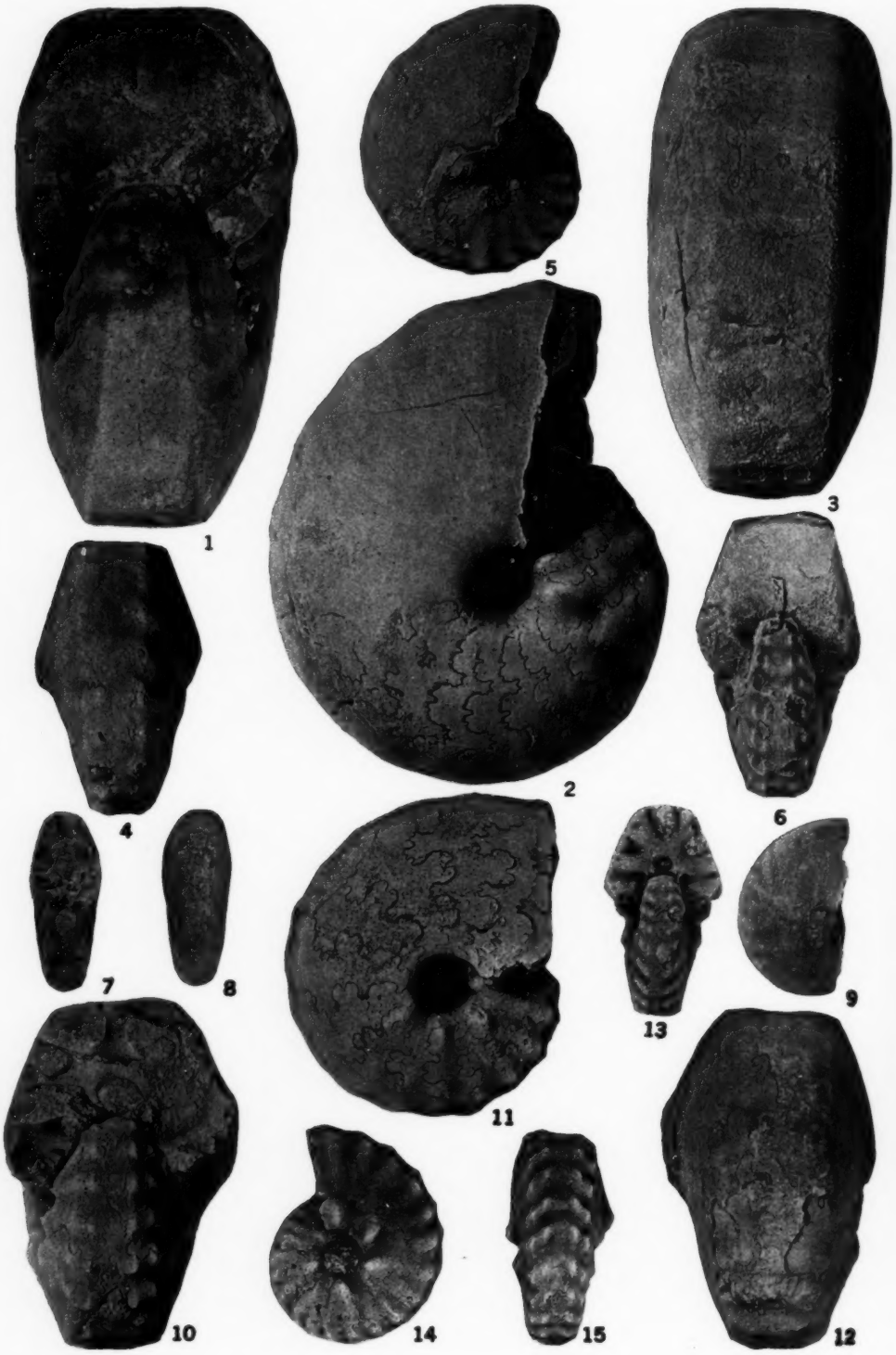
Kummel and Decker, Lower Turonian ammonites



Kummel and Decker, Lower Turonian ammonites

about 200 yards south of Needle Peak, locality 2612, Adkins (1931, p. 38).

Genus FAGESIA Pervinquière, 1907

Type species.—*Olcostephanus superstes* Kossmat, 1895.

This genus can be briefly diagnosed as follows. Conch evolute, umbilicus deep, umbilical walls steep, whorl section coronate with lateral ribs and blunt umbilical tubercles. Suture ammonitic, with very deep narrow, much indented elements. The genus *Fagesia* has a world-wide distribution and is lower Turonian in age. It has been recorded from India, Egypt, Tunis, France, Japan, Mexico, and in the United States in Texas and California.

FAGESIA TEXANA Adkins
Plate 32, figures 1, 2; text figure 2

Fagesia texana ADKINS, 1931, Univ. Texas Bull. 3101, p. 55, pl. 2, figs. 4, 10, 15.

The holotype of Adkins' species is available for study. The form is inflated and subglobose. The section of the last whorl is depressed with the venter and flanks gently rounded. The whorls are moderately embracing. The younger whorls are ribbed and have nodes on the umbilical shoulders. There are approximately six nodes per volution. From each node arises a pair of ribs that cross the venter and are slightly directed forward. Between each pair of ribs arising from a node are three similar ribs becoming evident higher on the flank and crossing the venter parallel to the forementioned ribs. There are approximately fifteen ribs per half-volution. The adoral part of the shell is almost smooth. The umbilicus is deep, with a vertical umbilical wall and moderately rounded shoulder. The dimensions of this specimen are: maximum diameter—60 mm., width of last whorl—36 mm., height of last whorl—23 mm., width of umbilicus—16 mm.

There are in the suture three lateral saddles and two lateral lobes on the flanks with a third lobe on the umbilical wall. The ventral lobe is asymmetrical and is taller than the first lateral lobe. It is divided by a low, quadrate saddle. The lobes decrease in height from the ventral lobe.

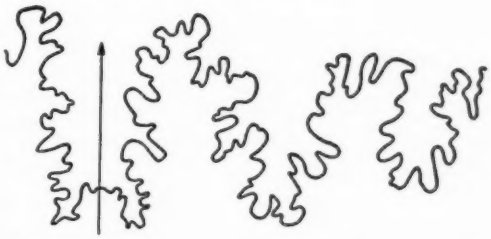


FIG. 2.—*Fagesia texana* Adkins. Diagrammatic representation of the external suture of the holotype at a diameter of 60 mm. ×2.

This species has a close resemblance to *Fagesia thevestensis* (Peron). The form and ornamentation of the two species are almost identical, but the suture line of *Fagesia texana* is less digitate, the ventral median saddle is much shallower, the external lobules of the first lateral saddles are enlarged, and a bifid saddle exists on the umbilical shoulder.

Holotype.—Bureau of Economic Geology, University of Texas.

Occurrence.—Chispa Summit formation, east side of Glenn Creek in the western foothills, southwestern Van Horn Mountains, Culberson County, Texas (see Adkins, 1931, p. 40).

FAGESIA HAARMANNI Böse
Text figure 3

Fagesia haarmanni BÖSE, 1920, Univ. Texas Bull. 1856, p. 211, pl. 14, figs. 1, 2; pl. 15, fig. 2.

One complete specimen and one fragment are in hand. The conch is involute with whorls much broader than high. The venter is very broadly arched passing without any break to the umbilical shoulder. Large nodes are present on the umbilical shoulder. From these nodes radiate flat, broad, rounded ribs which cross the venter without diminishing

EXPLANATION OF PLATE 31

FIGS. *1–15*—*Spathites chispaensis* Kummel & Decker, n. sp. Five specimens showing the surface ornamentation and the suture at various stages of growth. All specimens from the Chispa Summit formation, Placer de Guadalupe district, Mexico. *1–6*, *10–12*, ×1; *7–9*, ×3; *13–15*, ×2. (p. 311)

and are directed slightly toward the aperture. On the complete specimen one or two ribs arise from each node and one or two ribs are intercalated between the nodal ribs. The nodes are more numerous on the internal whorls where there appear to be about eight nodes per volution. The umbilicus is wide and deep, with a steep umbilical wall. The dimensions of the complete specimen are: maximum diameter—91 mm., width of the last whorl—53 mm., height of the last whorl—36 mm., and width of the umbilicus —30 mm.

The suture is partly present on the fragmentary specimen. It shows the ventral lobe, the first lateral saddles and the first lateral lobe. The ventral lobe is divided by a deep quadrate ventral saddle. The first lateral lobe is somewhat taller than the ventral lobe and is deeply and asymmetrically bifid, with the internal lobule longer and more prominent. The first lateral saddle is tall, rather narrow and trifid. The type specimens described by Böse (1920, p. 211) did not have the sutures preserved. The complete specimen recorded here is distorted and shows no more of the conch features than Böse's illustrations (1920, pl. 14, figs. 1, 2; pl. 15, fig. 2). The fragmentary specimen, however, does show at least part of the suture (Fig. 3).

FIG. 3.—*Fagesia haarmanni* Böse. Diagrammatic representation of the external suture at a whorl height of 37 mm. ×1.

The ribbing of this species resembles *Fagesia thevestensis* (Peron), but the ventral lobe of *F. thevestensis* is longer than the first lateral lobe, while the opposite is true of *F. haarmanni*. The species resembles *Fagesia superstes* Kossmat (1895) in the width of umbilicus and general form, but *F. superstes* has no nodes on the internal whorls as in *F. haarmanni*. *Fagesia californica* Anderson (1931) is similar to *F. haarmanni* but has a narrower whorl section.

Pleisotypes.—W. S. Adkins collection.

Occurrence.—Salmurian zone on the road from Acatita to Cuatro Ciénegas, in a narrow canyon some 15 kilometers west of the ranch of Piedra de Lumbre, Coahuila, Mexico.

FAGESIA sp.

Plate 33, figures 4, 5; text figure 4

Only one slightly distorted specimen is available. The conch is evolute, whorl section coronate, depressed. The venter is broadly rounded. The greatest width of the whorl is at the umbilical shoulder. There are prominent umbilical tubercles from which ribs project adorally and cross the venter. There are approximately 15 tubercles on the most adoral volution. Between the ribs originating from umbilical tubercles are single secondary ribs beginning just above the umbilical shoulder and becoming of equal strength to the primary ribs on the venter.

The suture is not preserved.

The dimensions of this specimen are: maximum diameter—86 mm., width of the

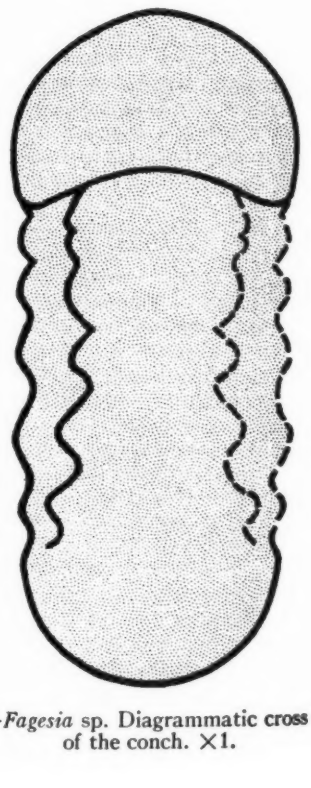


FIG. 4.—*Fagesia* sp. Diagrammatic cross section of the conch. ×1.

last whorl—38 mm., height of the last whorl —30 mm., and width of the umbilicus—40 mm.

The ribbing of this species resembles the ribbing of *Fagesia thevestensis* (Peron), but only one rib arises from each tubercle, as compared to two or three ribs arising from each tubercle of *F. thevestensis*. The number of tubercles compares very closely between these two species. The form of cross-section of *Fagesia thevestensis* is much thicker than that of this species. *Fagesia californica* Anderson (1931) has a similar cross-section but differs in ribbing, is more evolute and the tubercles are a little above the umbilical shoulder. *Fagesia siskiyouensis* Anderson is most similar to this specimen; however it has finer and greater density of ribbing.

Plesiotype.—Bureau of Economic Geology, University of Texas.

Occurrence.—Salmurian zone on the road from Acatita to Cuatro Ciénegas, in a narrow canyon some 15 kilometers west of the ranch of Piedra de Lumbre, Coahuila, Mexico.

Genus NEOPTYCHITES Kossmat, 1895

Type species.—Ammonites telinga Stoliczka, 1865=*Ammonites cephalotus* Courtiller, 1860.

This genus can be briefly diagnosed as follows. Conch very involute, venter arched, greatest width of whorls at umbilical edge. Inner whorls untuberculate. Low, broad ribs if present disappear soon, outer whorls smooth, generally compressed and constricted near aperture. Suture as in *Vascoceras*. *Neoptychites* is known from lower Turonian strata of France, North Africa, southern India, and Texas.

NEOPTYCHITES cf. N. XETRIFORMIS Pervinquière

Plate 32, figure 3; text figures 5, 6

Neoptychites sp., aff. *N. gourguchoni* ADKINS, 1931, Univ. Texas Bull. 3101, p. 57, pl. 2, figs. 18, 20.

Only one incomplete specimen is available for study. The conch is involute with a somewhat inflated discoidal form. The whorl section is tall, ovate, and has a maximum thickness near the umbilical shoulder. On the flanks are faint radiating broad distant ribs directed adorally which cross the venter. The conch is smooth except for the above mentioned ribs. The umbilicus is narrow and deep with the umbilical shoulder sharply rounded. The dimensions are: maximum diameter—65 mm., width of last whorl —29 mm., height of last whorl—35 mm., and width of umbilicus—8 mm.

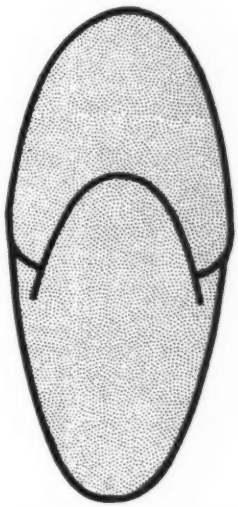


FIG. 5.—*Neoptychites* cf. *N. xetriformis* Pervinquière. Diagrammatic cross section of the conch of the specimen figured on plate 32, fig. 3. ×1.

The suture is similar to that of *Vascoceras*. There are three saddles and three lobes on the flank (Fig. 6). The first lateral saddle is broad and with a few distinct lobules. The second lateral saddle is smaller and divided by only two lobules, the external one being the larger. The first auxiliary saddle is smaller than the second lateral. A fourth saddle is on the umbilical wall. The ventral lobe is shorter than the first lateral lobe and has a wide quadrate median saddle. The first lateral lobe is slender, asymmetrically bifid, and much longer than the second

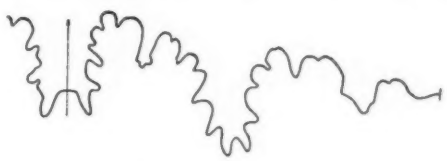


FIG. 6.—*Neoptychites* cf. *N. xetriformis* Pervinquière. Diagrammatic representation of the external suture at a whorl height of 29 mm. ×2.

lateral lobe. The first auxiliary lobe is oblique and pointed. The saddles are wider than the lobes.

Remarks.—Adkins (1931, p. 57) interpreted the following affinities for this genus:

> In form and suture this ammonite resembles *N. gourguchoni* Pervinquière and *N. perovalis* (von Koenen), with, however, important differences: the saddles are broader than tall; the third saddle is narrower than the second; the lobes are less inflected; the siphonal lobe is practically as long as the first lateral lobe; the third lobe is undivided and not oblique. This suture greatly resembles that of young *Neoptychites*. This resemblance and the similarity of form seem to justify the generic identification, but more material is necessary for specific determination.

We believe this specimen lies closest to the *Neoptychites xetriformis*. The swellings and grooves described by Pervinquière (1907) show a close similarity to the ribs on this specimen and the suture line resembles that of a young *Neoptychites xetriformis*. However, as stated by Adkins, more material is necessary for a specific determination.

Pleisotype.—Bureau of Economic Geology, University of Texas.

Occurrence.—Chispa Summit formation, east side of Glenn Creek in the western foothills, southwestern Van Horn Mountains, Culberson County, Texas (see Adkins, 1931, p. 40).

Family TISSOTIIDAE Hyatt, 1900
Subfamily PSEUDOTISSOTIINAE Hyatt, 1903

"HOPLITOIDES" ADKINSI Kummel & Decker, n. sp.

Plate 32, figure 6; plate 33, figure 3; text figures 7, 8

Hoplitoides (?) *mirabilis* Böse (not Pervinquière), ADKINS, 1931, Univ. Texas Bull., 3101, p. 59, pl. 4, fig. 2.

In our possession are six specimens which Adkins (1931, p. 59) compared with *Hoplitoides* aff. *H. mirabilis* Böse (1920, p. 225, pl. 19, figs. 1–3). The specimens are not well preserved. The conch is evolute, compressed and with a rounded venter on the body chamber. The whorl sides are broadly convex, ventral shoulders broadly rounded. The umbilical shoulder is sharply rounded, the umbilical wall almost vertical and high. The early volutions have a tricarinate periphery. The change from the tricarinate periphery to a smooth, rounded venter takes place at approximately a diameter of 100 mm. The measurements of three of the specimens are as follows:

	Holotype mm.	Paratype mm.	Paratype mm.
Maximum diameter	121	123	128
Width of last whorl	32	31	38
Height of last whorl	40	38	44
Width of umbilicus	38	39	39

The outer volution appears to have been devoid of any sculpture. The inner volutions appear to have distant, broadly rounded lateral ribs. The suture has two lateral lobes and three lateral saddles. The saddles are broad and with few blunt lobules.

Remarks.—As already indicated by Adkins (1931, p. 59) this species is not a *Hoplitoides*. It undoubtedly deserves a separate generic name but the material available and its preservation does not warrant this step at the present time. The species seems to be most closely related to "*Hoplitoides*" *nigeriensis* Wood (1911) from lower Turonian strata of Nigeria. Wood's species is more involute than "*H.*" *adkinsi*, the umbilicus being only one-seventh the diameter of the conch. "*Hoplitoides*" *nigeriensis* has a well developed tricarinate periphery. The only illustration of Wood's "*H.*" *nigeriensis* (pl. 23, fig. 3; pl. 24, fig. 1) is a septate specimen. He likewise makes no mention as to whether the peripheral carination decreases on the

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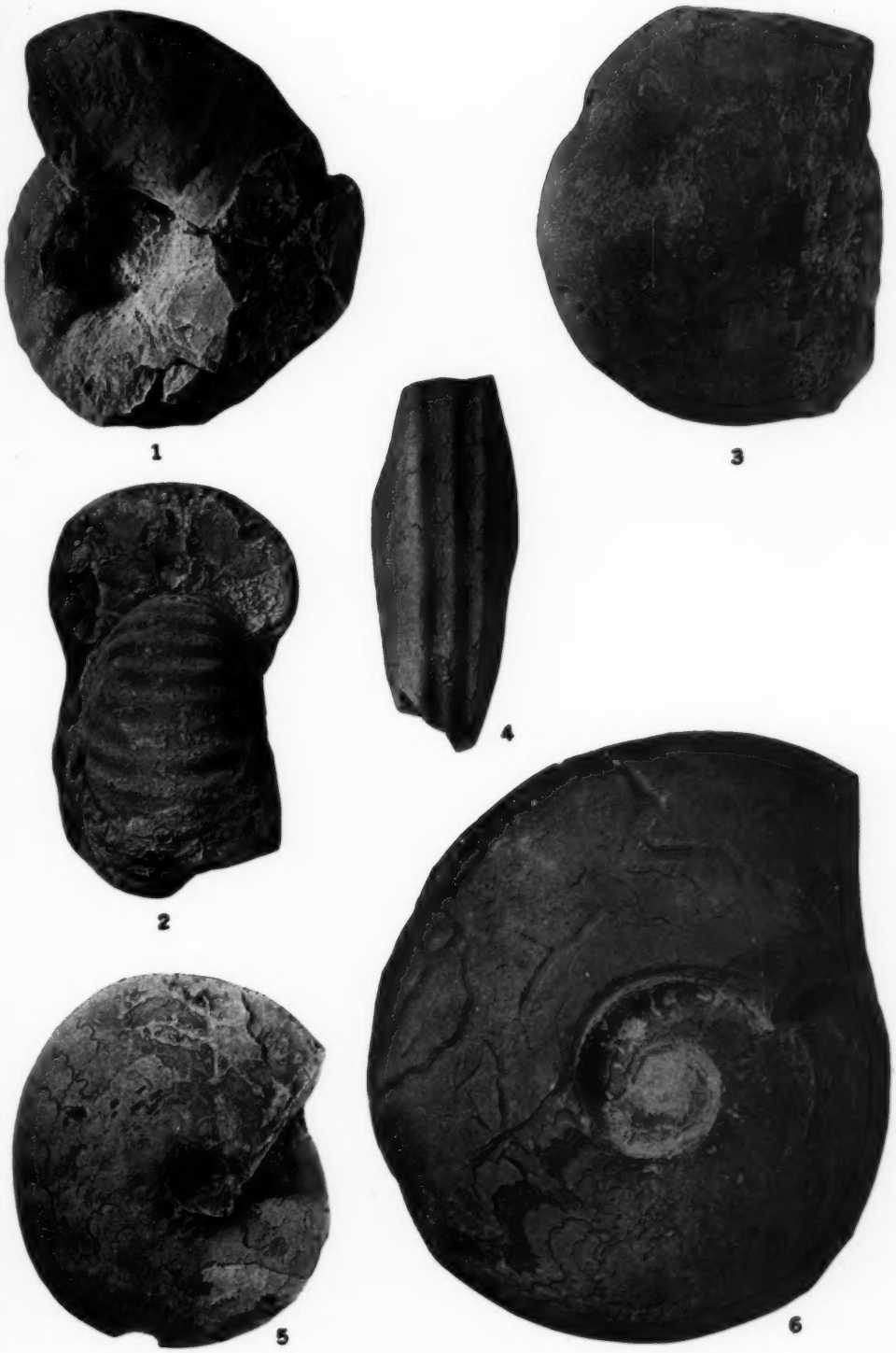
EXPLANATION OF PLATE 32

FIGS. *1, 2*—*Fagesia texana* Adkins. Lateral and apical views of holotype, Chispa Summit formation in Culberson County, on west flank of Van Horn Mountain, west Texas, ×1. (p. 313)

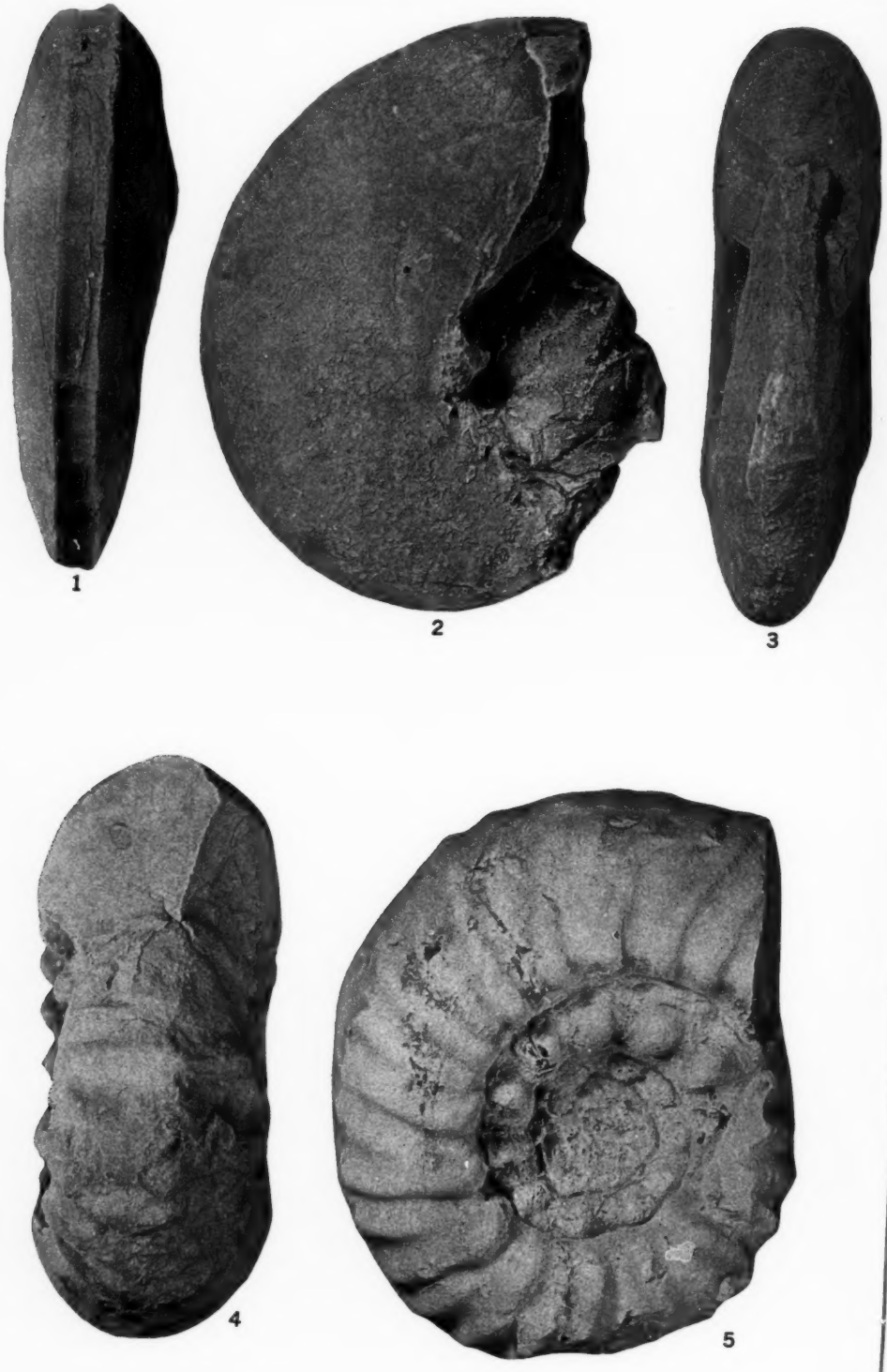
3—*Neoptychites* cf. *N. xetriformis* Pervinquière. Lateral view of specimen from same locality as figures *1, 2*, ×1. (p. 315)

4, 5—"*Hoplitoides*" *nigeriensis* Wood. Ventral and lateral views of immature specimen from Nigeria, ×1. (p. 319)

6—"*Hoplitoides*" *adkinsi* Kummel & Decker, n. sp. Lateral view of holotype from Piedra de Lumbre, Coahuila, Mexico, ×$\frac{3}{4}$. (p. 316)



Kummel and Decker, Lower Turonian ammonites



Kummel and Decker, Lower Turonian ammonites

body chamber. A small septate specimen of "*H.*" *nigeriensis* from Nigeria, kindly loaned to us by W. S. Adkins, is illustrated on Plate 32, figs. 4, 5; text figs. 7, 9.

"*Hoplitoides*" *adkinsi* loses the peripheral carination at an approximate diameter of 100 mm., after which the venter is broadly rounded. The tendency to smoothness of the peripheral region on the adoral volutions is typical of the whole superfamily to which this group belongs. The early volutions of "*H.*" *nigeriensis* bear rounded, distant, lateral ribs, similar to those of "*H.*" *adkinsi*. The sutures of these two species are also very similar. The suture is visible in small portions of one specimen of "*H.*" *adkinsi*. It is fairly complete except for the ventral lobe on the holotype, and not at all on the third specimen. Even on the holotype, however, the surface of the conch is slightly weathered. The large first lateral lobe is characteristic of these two species.

"*Hoplitoides*" *adkinsi* is likewise similar to *Vascoceras barcoicensis* Choffat (1898, pl. 17, fig. 1, pl. 18, fig. 1, pl. 22, figs. 35–36) in conch shape and degree of involution. *Vascoceras barcoicensis* has faint ventral ribs and the elements of the suture are more incised.

Types.—Bureau of Economic Geology, University of Texas.

Occurrence.—Holotype and paratypes from Salmurian zone on road from Acatita to Cuatro Ciénegas, in a narrow canyon some 15 kilometers west of the ranch of Piedra de Lumbre, Coahuila, Mexico. One poorly preserved specimen is from the Chispa Summit formation, on the west foot of Van Horn Mountains, 11 miles west and 1 mile north of Chispa station; collected by C. L. Baker, 1922.

"HOPLITOIDES" cf. "H." MUNIERI Pervinquière

Plate 33, figures 1, 2; text figures 7, 10

Two very well preserved specimens warrant distinct treatment. Like with "*Hoplitoides*" *adkinsi*, n. sp., these forms do not belong in *Hoplitoides* but need a new generic name. The material at hand, however, does not enable a thorough diagnosis of the group.

The conch is involute, highly compressed, lateral area convex and converging. The venter is truncate and concave, the ventrolateral shoulders are angular and slightly raised forming distinct keels. Low, indistinct irregularly spaced transverse ribs cross the venter. The holotype, consisting of both phragmocone and body chamber, shows no change in the degree of concavity of the truncate venter. The paratype has only a small portion of the body chamber preserved. The concavity of the truncate venter is much less than in the holotype and appears to decrease adorally.

The phragmocone has low, distant, radial ribs which are most conspicuous toward the venter. On the body chamber are very indistinct, low, broad folds.

The umbilicus is very small, the umbilical shoulders sharply rounded. The body chamber is more than one-half volution in length. The measurements of the specimens are as follows:

	Holotype mm.	Paratype mm.
Maximum diameter of conch	82	88
Width of last whorl	23	27
Height of last whorl	40	48
Width of umbilicus	6	7

The suture consists of irregularly incised lobes and saddles. The ventral lobe is narrow. The first lateral saddle is broad and divided by a distinct lobule. The first lateral lobe is the largest lobe, longer and broader than the ventral lobe, and with a conspicuous median division. The remaining lobes and saddles are small, the lobes being narrow, short and the saddles broad and smooth except for occasional blunt incisions.

Remarks.—"*Hoplitoides*" cf. "*H.*" *munieri* belongs to the group of "*Hoplitoides*" *munieri* and "*H.*" *mirabilis* Pervinquière

EXPLANATION OF PLATE 33

FIGS. *1, 2*—"*Hoplitoides*" cf. "*H.*" *munieri* Pervinquière. Ventral and lateral views of specimen from Cuchillo Parado, northern Mexico, ×1. (p. 317)

3—"*Hoplitoides*" *adkinsi* Kummel & Decker, n. sp. Apertural view of holotype from Piedra de Lumbre, Coahuila, Mexico, ×⅔. (p. 316)

4, 5—*Fagesia* sp. Apical and lateral views of specimen from Piedra de Lumbre, Coahuila, Mexico, ×1. (p. 314)

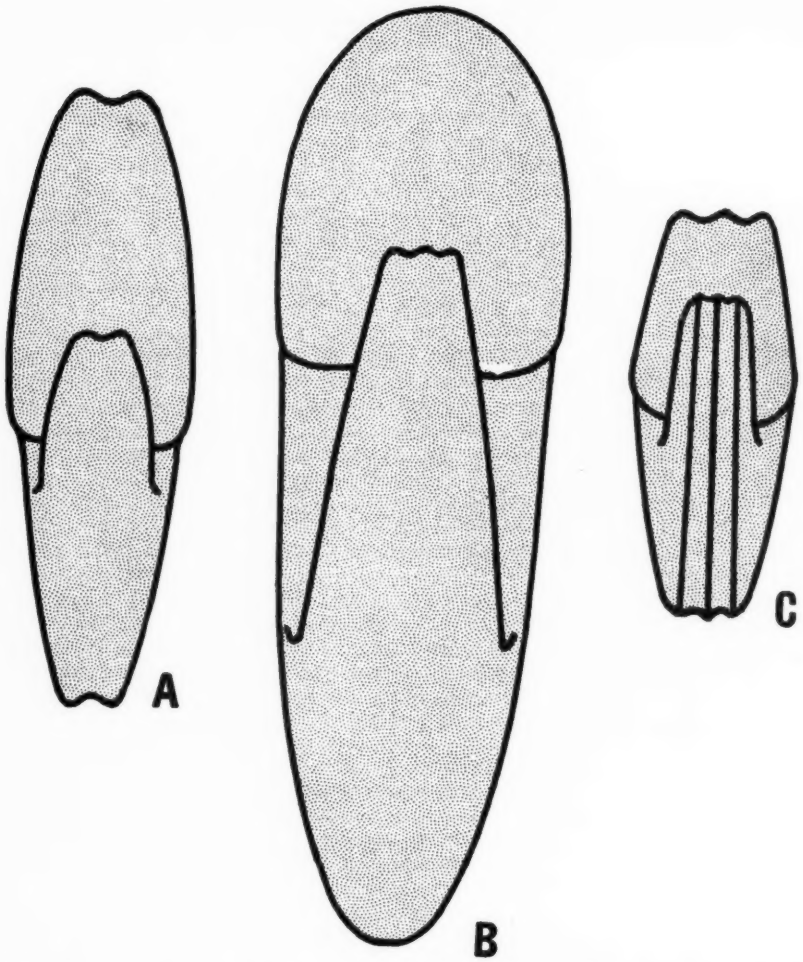


FIG. 7.—Diagrammatic cross section of the conch of: A. "*Hoplitoides*" cf. "*H. munieri* Pervinquière, ×1; B. "*Hoplitoides*" *adkinsi*, n. sp., ×1; C. "*Hoplitoides*" *nigeriensis* Wood, ×1.

(1907). These are the bicarinate group of "*Hoplitoides*" of Pervinquière (1907, p 217). "*Hoplitoides*" *munieri* and "*H.*" *mirabilis* are from Lower Turonian strata of Tunisia. Both these species are very similar in their conch shape to "*H.*" cf. "*H.*" *munieri*. The African species do not show any concavity of the truncate venter and have no ribbing. The width of the truncated venter is likewise less in the African species than in the species described here. Pervinquière (1907) separated "*H.*" *munieri* and "*H.*" *mirabilis* on the basis of differences in their suture. The incisions of the first lateral saddle and first lateral lobe of "*H.*" *mirabilis* are much more prominent than in "*H.*" *munieri*. The suture of "*H.*" cf. "*H.*" *munieri* is most similar to that of "*H.*" *munieri*. The ventral lobe of "*H.*" cf. "*H.*" *munieri* is confined to the venter, while in both the African species the ventral lobe extends beyond the ventrolateral shoulders. In general the incisions of the suture of "*H.*" cf. "*H.*" *munieri* are more irregular than in "*H.*" *munieri*.

Böse (1920) described two poorly preserved specimens as *Hoplitoides* aff. *H. mirabilis* Pervinquière from lower Turonian strata on the Cerro del Macho, Hacienda del

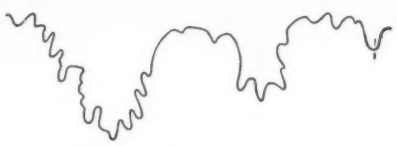


FIG. 8.—*"Hoplitoides" adkinsi*, n. sp. Diagrammatic representation of the external suture of the holotype figured on plate 32, fig. 6, at a diameter of 100 mm. Slightly larger than ×1.

Mohovano, Coahuila, Mexico. Even though the preservation of these specimens leaves much to be desired it seems clear from Böse's description and illustrations that his specimens are congeneric, if not conspecific with "*H.*" cf. "*H.*" *munieri.*

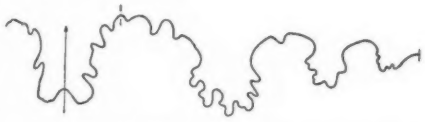


FIG. 9.—*"Hoplitoides" nigeriensis* Wood. Diagrammatic representation of the external suture of plesiotype figured on plate 32, figs. 4, 5. ×1.6.

Present studies on a large Turonian fauna from Nigeria by a French student indicate that the group of *"Hoplitoides" nigeriensis* Wood, the tricarinate forms, and the group of *"Hoplitoides" munieri*, the bicarinate forms, are transitional (C. W. Wright, personal communication). The relationships of our bicarinate species of *"Hoplitoides"* to the African forms are very close. There is likewise no question but that these *"Hoplitoides"* deserve separate generic status.

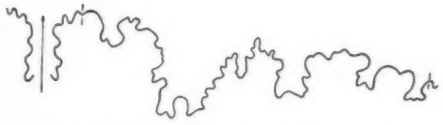


FIG. 10.—*"Hoplitoides"* cf. *"H." munieri* Pervinquière. Diagrammatic representation of external suture of unfigured specimen. Slightly larger than ×1.

MANUSCRIPT RECEIVED MAY 21, 1953

Types.—Holotype and paratypes, Bureau of Economic Geology, University of Texas.

Locality and position.—Exact locality and zone unknown, specimens from near Cuchillo Parado, northern Mexico.

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JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 3, PP. 320–324, PLS. 34–35, MAY 1954

JURASSIC NAUTILOIDS FROM WESTERN NORTH AMERICA

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ABSTRACT—Three new species of nautiloids from western North America are figured and described: *Eutrephoceras montanensis*, *Bisiphytes* (*Cenoceras*) *imlayi*, and *B.* (*C.*) *lupheri*. The specimens came from the Rierdon formation of Montana, the Weburg formation of Oregon, and the Kialagvik formation of the Alaskan Peninsula. Only two species of Jurassic nautiloids have previously been reported from North America. *Cenoceras* Hyatt is placed as a subgenus of *Bisiphytes* Montfort.

INTRODUCTION

NAUTILOIDS from Jurassic formations are very uncommon fossils, especially so in North America. The richly fossiliferous Jurassic formations of Europe and Asia have yielded relatively few species and genera of nautiloids compared to the richness of the ammonite faunas. The nautiloids became almost extinct near the close of the Triassic. The evolutionary history of Triassic nautiloids can be summarized as a culmination of trends that began in the Carboniferous. The high degree of ornamentation attained in some stocks of Triassic nautiloids was never again repeated in the evolution of this group. Early in the Jurassic new stocks and evolutionary patterns were quickly established. There is no "break" in the evolutionary pattern of the nautiloids from the Jurassic to the Cretaceous.

Our knowledge of Jurassic nautiloids progresses very slowly. The only classification of post-Triassic nautiloids is that of Spath (1927). The literature on Jurassic nautiloids is sparse and is generally only a small part of larger faunal studies. Papers devoted entirely to Jurassic nautiloids include those by Parona (1897), Crick (1898), Tagliarini (1901), Prinz (1906), Pia (1914), and Loesch (1914).

The collection under study consists of only 15 specimens that include *Bisiphytes* (*Cenoceras*) *imlayi*, n. sp., from the Kialagvik formation of Alaska (lower Bajocian age); *Bisiphytes* (*Cenoceras*) *lupheri*, n. sp., from the Weburg formation of Oregon (lower Bajocian); *Eutrephoceras montanensis*, n. sp., from the Rierdon formation (Callovian) of Montana; and *Eutrephoceras* sp. indet. from the Twin Creek limestone (Bajocian) of Wyoming.

The only other described species of nautiloids from the Jurassic of North America are "*Nautilus*" *burkarti* Castillo and Aguilera (1895) and "*Nautilus*" *naufragus* Cragin from the Malone formation of Texas (Cragin, 1905). "*Nautilus*" *burkarti* belongs in *Eutrephoceras*. The proper generic assignment of "*Nautilus*" *naufragus* cannot be told from Cragin's description or illustrations.

All of the specimens have been collected by R. W. Imlay of the U. S. Geological Survey with various associates. The writer is indebted to Imlay for the opportunity to study these specimens. The holotype of *Bisiphytes* (*Cenoceras*) *imlayi*, n. sp., was photographed for the writer by A. K. Miller and C. Collinson at The State University of Iowa.

SYSTEMATIC DESCRIPTIONS

Family NAUTILIDAE d'Orbigny, 1840

Genus EUTREPHOCERAS Hyatt, 1894

EUTREPHOCERAS MONTANENSIS Kummel, n. sp.

Plate 34, figures 1, 2

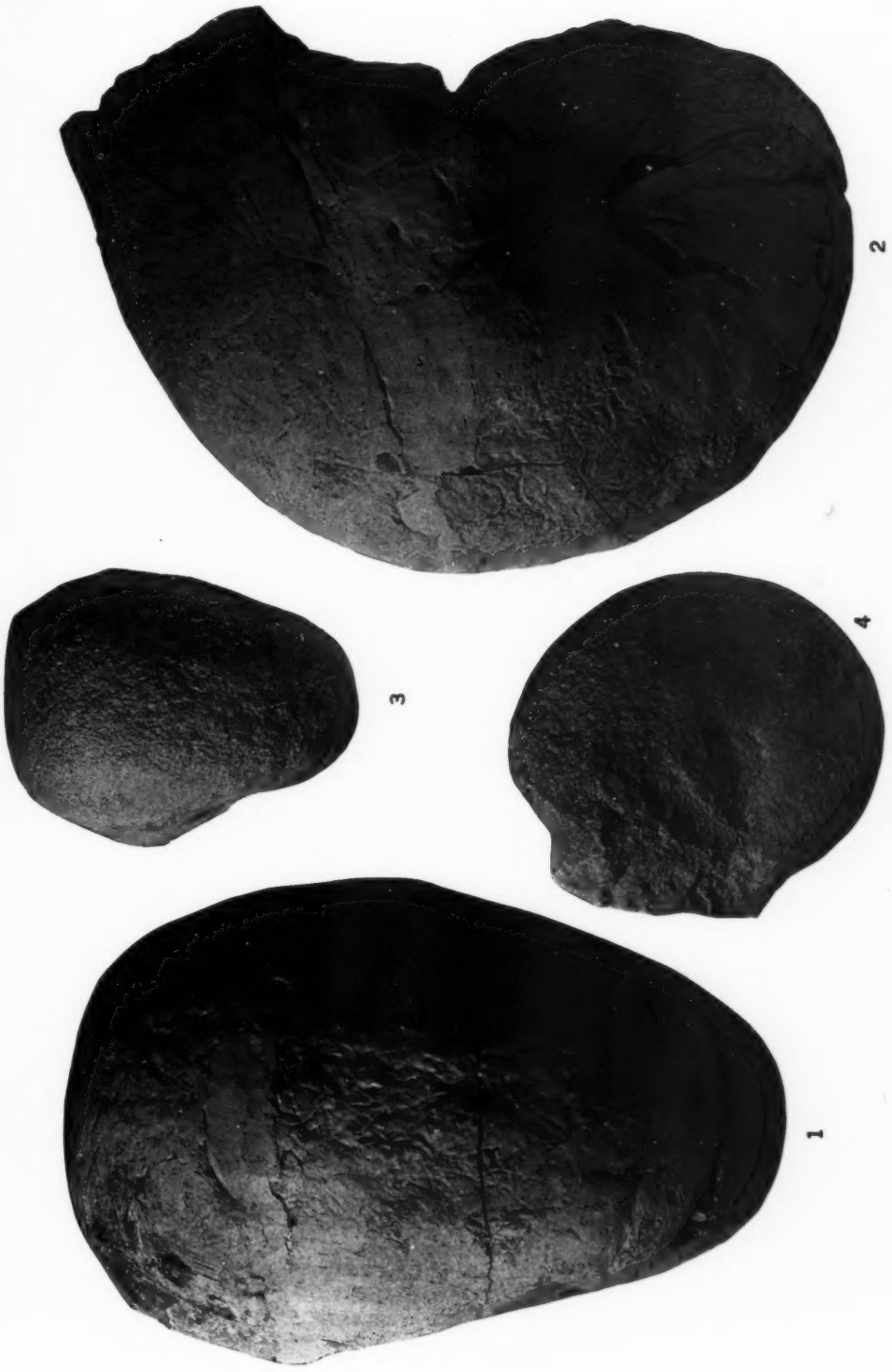
Type species.—*Nautilus dekayi* Morton.

The Rierdon formation in Montana has

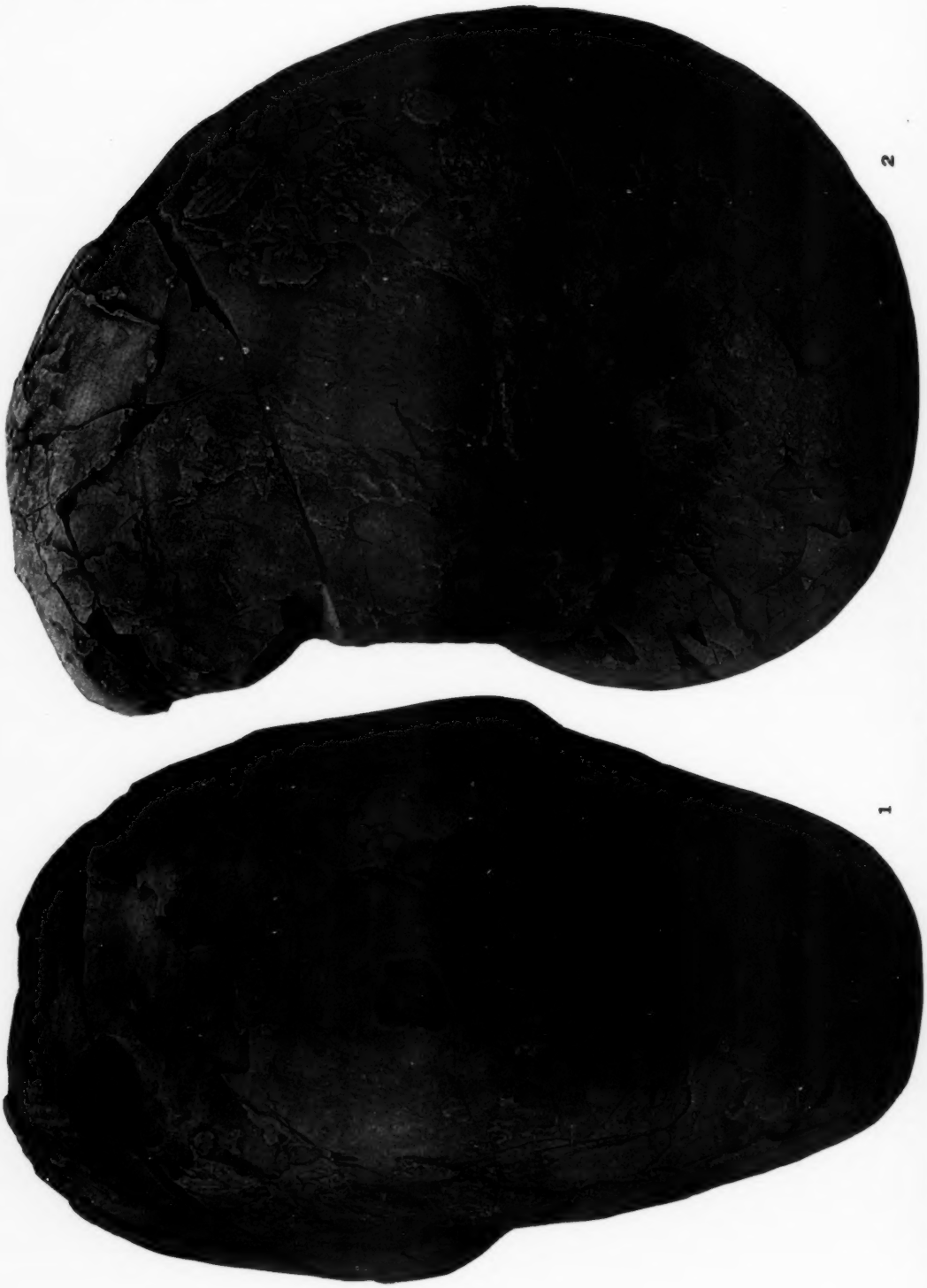
EXPLANATION OF PLATE 34

FIGS. *1, 2*—*Eutrephoceras montanensis* Kummel, n. sp. The holotype (USNM) from the Rierdon formation, Fergus County, Montana (U.S.G.S. loc. 19170), ×0.5. (p. 320)

3, 4—*Bisiphytes* (*Cenoceras*) *lupheri* Kummel, n. sp. The holotype (USNM) from the Weburg formation, Grants County, Oregon (U.S.G.S. loc. 21612), ×0.5. (p. 323)



Kummel, Jurassic nautiloids



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Kummel, Jurassic nautiloids

yielded 10 specimens of nautiloids that are a new species of *Eutrephoceras*. The specimens are internal molds and for the most part partially crushed. The largest and best preserved specimen (U.S.G.S. loc. 19170, Pl. 34, figs. 1, 2) is designated the holotype. It measures 203 mm. in diameter and consists of a complete phragmocone plus a half whorl of living chamber. The most adoral part of the living chamber is 138 mm. wide and 188 mm. high. The conch is very involute and rapidly expanding. The whorl section is higher than wide on the phragmocone, but becomes depressed on the living chamber. The whorl sides are broadly rounded passing gradually onto a broadly rounded venter. The widest part of the whorl section is just above the umbilical shoulder. The umbilical shoulder is more sharply rounded and passes to a steep, high umbilical wall. On the internal mold there is a small umbilicus present. The suture is nearly straight across the venter and forms a very shallow lobe on the whorl sides. The siphuncle is located slightly below the center of the whorl.

Remarks.—Species of *Eutrephoceras* have long been recognized from the Cretaceous and the Cenozoic. However, there are several species in the Jurassic that properly belong in this genus. Spath (1927, p. 23) would include *Nautilus obesus* Sowerby from the Bajocian of Europe. Most certainly *N. cyclotus* Oppel (Zittel, 1868, pl. 3, figs. 2a, b) from the Upper Jurassic of central Europe belongs in *Eutrephoceras*. I would also include *N. rotundus* Crick (1898, p. 132) and *N. subrotundus* Crick (1898, p. 133) from the Inferior Oölite of England. *N. boissieri* Pictet (1867) and *N. bradfordensis* Crick (1898, p. 117) have more compressed conches, but can well be included within *Eutrephoceras*. *Nautilus waageni* Gemmellaro (1886), *N. lutati* Gemmellaro (1886), *N. mazzarensis* Tagliarini (1901) from the lower Dogger of Italy should also be placed in *Eutrephoceras*. *Nautilus burkarti* Castillo and Aguilera (1895, p. 12) from the Upper Jurassic of Mexico and the Malone Mountains of Texas (Cragin, 1905) also belong in *Eutrephoceras*.

Occurrence.—Upper Jurassic, Callovian, Ellis group, Rierdon formation, Montana.

U.S.G.S. loc. 19170, from lower 15 feet of Rierdon formation—*Gowericeras subitum* zone—slightly north of center of sec. 15, T. 14 N., R. 21 E., Fergus County; U.S.G.S. loc. 18758, *Kepplerites mclearni* zone, Section Creek, sec. 1, T. 28 N., R. 20 E., Blaine County; U.S.G.S. loc. 9662, NW¼ sec. 14, T. 7 S., R. 24 E., Bridger Canyon; U.S.G.S. loc. 18726, W.½ sec. 7, T. 24 N., R. 25 E., Morrison Butte, Little Rocky Mountains; U.S.G.S. 19180, from 30 ft. of shale and nodular limestone just above ledge of sandy limestone about 1 mile southeast of Piper in SE¼ sec. 9 and NE¼ sec. 16, T. 14 N., R. 20 E., Fergus County; U.S.G.S. loc. 19586, about 24 feet above base of Rierdon formation, Chalk Butte dome, sec. 7, T. 25 N., R. 26 E., Little Rocky Mountains, Phillips County; U.S.G.S. 21636, about 25 feet above base of Rierdon formation on divide about ½ mile west of Five Mile Creek, sec. 36, T. 5 S., R. 24 E., Pryor Mountains, Carbon County.

Repository.—U. S. National Museum.

EUTREPHOCERAS sp. indet.

One fragmentary and weathered specimen of one half volution of phragmocone from the Twin Creek limestone of Wyoming is specifically distinct from *E. montanensis*, but too incomplete to establish a new species. The specimen's value is in the recording of *Eutrephoceras* from the Twin Creek limestone.

Occurrence.—U.S.G.S. loc. 20981, Middle Jurassic, Bajocian, Twin Creek limestone, from upper 20 feet of member B, about 150 to 170 feet above base of formation. From head of Leed Canyon, secs. 1 and 2, T. 22 N., R. 119 W., Lincoln County, Wyoming.

Repository.—U. S. National Museum.

EXPLANATION OF PLATE 35

FIGS. *1, 2*—*Bisiphytes* (*Cenoceras*) *imlayi* Kummel, n. sp. The holotype (USNM) from the Kialagvik formation, Alaskan Peninsula (U.S.G.S. loc. 21251), ×0.5. (p. 322)

Genus BISIPHYTES Montfort, 1802
Subgenus CENOCERAS Hyatt, 1884
BISIPHYTES (CENOCERAS) IMLAYI
Kummel, n. sp.
Plate 35, figures 1, 2

Two large and well-preserved specimens form the basis of this species. The holotype (pl. 35, figs. 1, 2) is a nearly complete internal mold with isolated portions of the shell preserved. This specimen is by far the best preserved of the Jurassic nautiloids described in this report. The paratype is fragmentary consisting of approximately ⅓ volution of living chamber and three camerae. It has much of the shell on the venter preserved.

The holotype measures 295 mm. in diameter and 185 mm. in width and 174 mm. in height of the most adoral part of the outer whorl. At the beginning of the living chamber the width-height measurements are 140 and 135 mm. respectively. The conch is large, robust, and very involute. The whorl sides are flattened to slightly arched and converge towards the venter. The venter is broadly arched on the phragmocone becoming more flattened adorally. The ventral shoulders are broadly rounded. The umbilical shoulders are likewise well rounded. The greatest width of the conch is just ventral of the umbilical shoulders. The umbilicus is very narrow.

The paratype (U.S.G.S. loc. 19757) is a much smaller specimen that probably had a diameter of 160 mm. It differs slightly from the holotype in that the whorl sides appear more flattened and the ventral shoulders more angularly rounded. The venter is flattened to broadly arched. The differences between the specimens are not thought to be of specific importance.

The suture forms a shallow ventral lobe and a wide shallow lateral lobe. The siphuncle is not observable on the holotype but on the paratype it is slightly ventral of the center of the whorl.

Only portions of the shell are preserved on both specimens but from these fragments, however, one can observe distinct growth lines and longitudinal striae. The striae on the holotype are approximately 1.5 mm. wide, as are also the interspaces between the striae. On the holotype there are patches of shell showing the striae on the venter, just below the ventral shoulder, and one just above the umbilical shoulder. Presumably the striae were on the whole shell, that is, on the whorl sides and venter. The striae are not noticeable on the internal mold. The venter of the paratype has about half of the shell preserved in a rather weathered condition; however, the longitudinal striae are very distinct and present over the ventral shoulder. Portions of the shell are preserved on one side of the conch just above the umbilical shoulder; the striae are not present on these shell fragments but strong growth lines are clearly shown.

Remarks.—There are differences in the shape of the conch and ornamentation between the two specimens described here. However, since they both come from the same formation and from very nearby localities and with no idea as to the range of variation that may be present, it is considered better to follow a more conservative course and place them in one species.

After a preliminary examination of this specimen I was inclined to place it in *Paracenoceras*; however, the presence of the longitudinal striae and the geologic age of the specimens suggest that it belongs in *Cenoceras*. The classification of Liassic and Bajocian nautiloids is at present very unsatisfactory. Most of the nautiloid species of these epochs are most conveniently placed in *Bisiphytes* or *Cenoceras*. *Bisiphytes* is typically involute and with a rounded whorl section and shell ornamentation consisting of growth lines and striations. *Cenoceras* is exactly like *Bisiphytes* in most morphologic features except for its more quadrate whorl sections. However, as Spath (1927, p. 20) has pointed out, Hyatt's genus *Cenoceras* has not been generally accepted. There are species which can be placed in either genus with about equal propriety. There are also species that agree with one or the other of these two genera in all features except they lack the longitudinal striae on any part of the shell. The variability in cross section of Liassic nautiloid species is well demonstrated in cross sectional outlines figured by Pia (1914, pls. 8–10). The gradational character of these two genera and the wide variation present suggest that they should be combined. However, phylogenetically there

are advantages in keeping separate the quadrate "*Bisiphytes*." For this reason it is proposed to make *Cenoceras* a subgenus of *Bisiphytes*.

The remaining species of Liassic nautiloids are included in *Sphaeronautilus*, *Digonioceras*, *Ophionautilus*, and *Hercoglossoceras*. These are aberrant genera that contain few species of limited distribution.

B. (*C.*) *imlayi* is similar to such early Jurassic species as *B.* (*C.*) *intermedium* (Sowerby), *B.* (*C.*) *jourdani* (Dumortier), *B.* (*C.*) *truncatus* (Sowerby), *B.* (*C.*) *quadrangularis* (Pia), *B.* (*C.*) *brancoi* Gemmellaro, *N. obstructus* Eudes-Deslongchamps. It differs from all of these species in details of whorl sections and involutions.

Occurrence.—Holotype, U.S.G.S. loc. 21251, Kialagvik formation—lower Bajocian age. From sandy sequence corresponding to *Hammatoceras kialagvikense* "subzone" of Kellum. Sea cliff on southeast shore of Wide Bay, 5.32 miles S. 46½°W. of the west end of Hartman Island. Grey siltstone containing many limestone concretions, about 500 feet below the top of the Kialagvik formation. Paratype, U.S.G.S. loc. 19757, from 975 to 800 feet below top of Kialagvik formation associated with *Erycites howelli* (White) and *Pseudolioceras whiteavesi* (White). Sea cliffs on northwest side of Wide Bay southwest of mouth of Pass Creek and about 3½ miles N. 50 W. of west end of Hartman Island, Alaskan Peninsula.

Repository.—U. S. National Museum.

Bisiphytes (Cenoceras) lupheri Kummel, n. sp.
Plate 34, figs. 3, 4

Two internal molds of rather coarse preservation from the Weburg formation of Oregon are in the collections under study. Lupher (1941, p. 248) mentions the occurrence of large nautiloids in the Weburg formation. The holotype (Pl. 34, figs. 3, 4) is a nearly complete specimen with a living chamber of ⅓ volution in length. The paratype is very poorly preserved and can add nothing to the description. The holotype measures 91 mm. in diameter, and the height and width of the most adoral part of the last volution are approximately 47 mm. and 67 mm. respectively. At the most adoral part of the phragmocone the height-width measurements are 37 mm. and 51 mm. The conch is very involute and somewhat compressed. The whorl sides are broadly convex to flattened and converge towards the venter which is broad and flattened. The ventral shoulders are broadly rounded. The umbilical shoulders are more abruptly rounded. The whorls are more rapidly expanding on the living chamber than on the phragmocone. The umbilicus measures approximately 16 mm. The suture is only moderately sinuous with a very shallow ventral lobe and a wide shallow lateral lobe that occupies the whole whorl side. The position of the siphuncle is not known.

No part of the shell is preserved.

Remarks.—This species is quite distinct from *B.* (*C.*) *imlayi* in the shape of the conch and its size. It is most similar to *B.* (*C.*) *intermedium* Sowerby and *B.* (*C.*) *orbignyi* Prinz (= *N. intermedius* d'Orbigny *non* Sowerby). The latter species was designated the type species of *Cenoceras* by Hyatt (1884, p. 301).

Occurrence.—U.S.G.S. loc. 21612, upper part of Middle Jurassic, Weburg formation, lower Bajocian age, just north of Colpitts Ranch in NE corner sec. 19, T. 18 S., R. 26 E., Grant County, Oregon.

Repository.—U.S. National Museum.

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JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 3, PP. 325–332, PLS. 36–37, 5 TEXT FIGS., MAY 1954

UNUSUAL DEVONIAN BRACHIOPODS[1]

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ABSTRACT—*Syringospira prima* Kindle, a rare spiriferoid from the Percha shale of New Mexico is redescribed. This brachiopod proves to have a frill extended laterally from the palintrope of the pedicle valve, the umbonal and delthyrial cavities occupied by cystose shell, and a hitherto unknown cover over the pedicle opening. It probably lived loose on the sea-bottom because its pedicle was atrophied. A related genus *Sphenospira* Cooper, n. gen., from the Conewango group of Pennsylvania and New York is described and based on *"Cyrtia" alta* (Hall).

INTRODUCTION

For many years the writer has been interested in the fauna of the Percha shale of New Mexico. This interest arose during his work on the Devonian Correlation Chart. The Percha shale proved difficult to correlate with other Upper Devonian faunas. Nevertheless a correlation was made with the lower portion of the Conewango Stage (Amity shale) (Cooper, 1942). The shale was dated "by the similarity of *Syringospira prima* [of the Percha shale] to '*Cyrtia*' *alta* of the Amity shale situated in the lower part of the Conewango stage." Although it was stated that Mississippian types also appear in the Percha shale, it was decided that the similarities of Percha fossils to those of the Conewango justified the correlation. The two brachiopods mentioned above are quite unusual and are nearly precisely alike in exterior details. The similarities are so great that the correlation was made without trepidation and had supporting evidence from other members of the faunas. Nevertheless the correlation was later challenged by Stainbrook (1947, p. 323) who maintained that *Syringospira* and *"Cyrtia" alta* are not alike. *Syringospira*, he said, differs from the New York and Pennsylvania species in "not having the fold and sulcus as strongly plicate and in lacking the pear-shaped delthyrial tube, no indication of which is shown in Hall's illustrations. *Syringospira prima* appears to be more specialized and, therefore, of younger age than *Spirifer altus*." Stainbrook is correct in his surmise that *Syringospira* is more specialized than *"Cyrtia" alta* but his belief that this specialization denotes a younger age is open to question.

The age of the Percha shale is still in question but the discovery by A. L. Bowsher of *Falciclymenia bowsheri* Miller (Miller, 1951) is fairly good evidence of Devonian age because the clymenids are not yet known from the Mississippian. It is possible that the Percha shale is more closely related to the Three Forks formation of Montana than hitherto suspected.

The difficulties of correlation and the intriguing problem of establishing the correct age of the Percha shale took the writer to Silver City and adjacent areas, New Mexico, where the shale is well exposed. Four visits were made to this region with the result that a superb collection of fossils was obtained which is expected to yield much new evidence on the stratigraphic and biological relationships of the brachiopods. Enough has already been done with the productellids from the Percha to say that no Mississippian genera are represented among them. One of the objectives of the field work in the Percha shale was to obtain a good set of specimens of *Syringospira*. Sufficient material was collected to demonstrate that this is a highly specialized brachiopod which is closely related to *"Cyrtia" alta* but differs from it in interior characters. The two however belong to the same family. Below are detailed the morphological characters of *Syringospira* and *Sphenospira*, a name here proposed for *"Cyrtia" alta* (Hall).

Genus SYRINGOSPIRA Kindle

Plate 36, figures 1–7, 11; plate 37, figures 1–18; text figures 1–4.

Syringospira KINDLE, 1909, U. S. Geol. Survey Bull. 391, p. 28. STAINBROOK, 1947, Jour. Paleontology, vol. 21, no. 4, p. 322.

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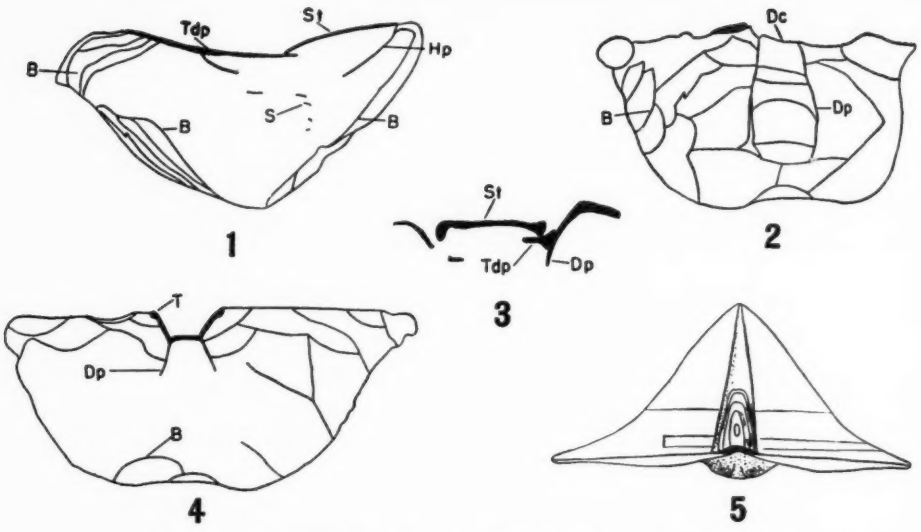

FIGS. *1–5*—*Syringospira prima* Kindle and *Sphenospira alta* (Hall)
Legend: B = blister, Dc = delthyrial cavity, Dp = dental plates, Hp = hinge-plate, S = spire, St = stegidium, T = tooth, Tdp = transverse delthyrial plate.

Syringospira prima Kindle. All from Percha formation (Box member), New Mexico. (p. 325)

FIG. *1*—Longitudinal section through a nearly complete specimen, ca. ×2. Hypotype USNM 123365c. Fork of Percha Creek, center north line section 16, T. 16 S., R. 8 W., on New Mexico highway 180, 2 miles east of Kingston.

2—Cross-section of the pedicle valve, ca. ×2, showing abundant blisters. Hypotype USNM 123361b. Hairpin bend at Georgetown, Silver City Quadrangle.

3—Section showing lateral extensions of the transverse delthyrial plate on inner side of the dental plates overlain by the distal end of the stegidium, ca. ×2. Hypotype USNM 123363c. 5.4 miles north of the junction of Atlantic and Alabama Streets, Silver City.

4—Cross-section of a pedicle valve taken near the living cavity of the animal, showing the transverse delthyrial plate, the section of a small rod made by growth of the teeth, the dental plate ridges and irregular and sporadic development of blisters, ca. ×2. Hypotype USNM 123368c. Four miles east of Santa Rita.

Sphenospira alta (Hall). Chagrin formation (8 to 20 feet below the Cleveland shale), Chippewa Creek, one mile east of Brecksville, Cuyahoga County, Ohio.

FIG. *5*—Reproduction based on described specimen to show form and extent of palintrope and cardinal extensions, ca. ×½.

Kindle based his species and genus on two specimens both of which are quite incomplete. A loose specimen of *Syringospira* picked up on the outcrop is usually an attractive collector's item because of its bizarre form but the most instructive and complete specimens should be taken bedded in matrix.

EXTERIOR FEATURES

Syringospira has unequal valves, that of the pedicle valve being an elongated half cone with a broad and flat, triangular interarea and a somewhat compressed surface opposite to the palintrope. In lateral profile the pedicle valve forms a narrow, sharply pointed wedge. The brachial valve is gently convex in lateral profile and broadly and gently convex in anterior profile, thus quite shallow. The pedicle valve is marked medially by a shallow sulcus that widens anteriorly. The floor of the sulcus is produced anteriorly as a short, rounded tongue. The beak of the brachial valve is broadly obtuse and is somewhat incurved over the delthyrium. The palintrope of the brachial valve is moderately long and usually projects more or less prominently in a direction posterior to the pedicle palintrope. The entire surface of both valves, except for the palintropes, is marked by closely crowded costae which are wider than the spaces separating them. The costae are covered, in well-preserved specimens, by small, elongate

pustules with the blunt end pointed anteriorly. These are most conspicuous on young specimens. Other features of the exterior need further elaboration (pl. 36, figs. 3, 4; pl. 37, figs. 1, 17).

Palintrope.—The interarea, or exterior surface of the palintrope (cardinal area of old terminology), is marked by narrowly rounded, straight, elevated lines running perpendicular to the hinge-line, and maintaining their perpendicularity regardless of irregularities. These lines meet the delthyrial margin and the posterior shell margin at acute angles. The ridges on the interarea of the pedicle valve are opposite ridges on the interarea of the brachial valve. These ridges are a feature of the outer shell-layer and do not crenulate the hinge-margin of either valve. Inasmuch as they are features of the outer layer they do not represent growth tracks of hinge-teeth as they do in some spiriferoids and spiriferinoids (*Spondylospira* for example). The possible value of these ridges to the animal is discussed under its life-habits (pl. 36, fig. 7; pl. 37, fig. 9).

One of the most remarkable features of *Syringospira* is the extension of the palintrope and the shell of the body part into a thin and wide flange. This extends laterally for a considerable distance and forms a broad flat base when the shell is set down on the interarea. The width of the flange varies in different specimens. The structure is a delicate one and is difficult to obtain in its complete form. In order to obtain this structure specimens must be taken in matrix as mentioned above. These extensions usually double the width of the shell and in some instances increase it even more. The extensions may or may not taper laterally. In at least two instances they appear to be abruptly truncated laterally. The interarea surface of the extension is marked like that of the main portion of the interarea but a horizontal element of lines of growth cancellates the perpendicular lines. The anterior surface is somewhat irregularly and transversely lamellose. The value of the frill to the animal is also discussed under its life-habits (pl. 36, figs. 1, 2, 5).

The largest specimen of *Syringospira*, USNM 123360, known to the writer is quite incomplete but measures 67 mm. at its widest points. The most nearly complete specimen of the pedicle valve, USNM 123361a, measures 43 mm. in width but the body of the shell, i.e., the part that would split off from the lateral flanges, is only 21 mm. wide. This means that the frill approximately doubles the shell-width. The largest specimen, when complete, must therefore have had a minimum width of approximately 120 mm. Another specimen has a somewhat longer extension of 20 mm. on each side of a shell-body 34 mm. wide. This is almost exactly half the width of the largest specimen mentioned above and suggests the possibility of a maximum width of nearly 150 mm. for the species.

Delthyrium and associated structures.—The interarea is traversed from beak to anterior margin by a gradually widening delthyrium which forms an angle at the apex of 10° to 20°, averaging about 15°. The delthyrial edge is marked by a slight thickening which represents the progressive growth path of the tooth or articular process. This thickened margin is often broken away in the weathered specimens available for study leaving a narrow groove along the delthyrial edge. A short distance below the delthyrial edge an elongate plate, the transverse delthyrial plate of Hall and Clarke (1894, pl. 26), closes the posterior two-thirds of the delthyrium. The plate ends anteriorly in a deep reentrant concave toward the brachial valve. The surface of the plate may be smooth or may show concentric, crescentic lines convex toward the beak, which represent resting stages in the forward growth of the plate. The largest specimen in the collection, USNM 123360, has an elevated ridge extending for the full length of the plate and located at about its center. This is not seen in the younger shells and may thus be an old age character. The position and nature of this delthyrial plate is like that common in many spiriferoids, especially the related *Eosyringothyris* and *Pseudosyrinx*. This plate extends for about two-thirds the length of the delthyrium from the apex. Anterior to it is a deep and large cavity, but this is closed by a second roofing plate which restricts the foramen produced by the sunken transverse delthyrial plate and eventually sealed the opening completely when the pedicle became functionless (pl. 37, fig. 4).

The second plate, here called STEGIDIUM from the Greek *stege*, roof, is moderately convex transversely and longitudinally and in length is about one-third the length of the delthyrium. It extends from and overlaps the distal margin of the transverse delthyrial plate. The stegidium is built of concentric layers, each one higher toward the brachial valve until the last forms a knot at the apex. The first layer is laid around the crescentic margin of the transverse delthyrial plate and extends along the margins of the delthyrium where the dental lamellae become considerably narrowed. The convex stegidium is then built up by concentric shells, each lying over the edge of the preceding one until the pedicle opening is completely sealed. The building of this plate is evidently an act of the adult animal which culminates in disappearance of the pedicle. As will be shown below several other features of the shell all tend to facilitate life without peduncular attachment to the substratum (pl. 37, figs. 6, 7, 14).

INTERIOR FEATURES

The interior of *Syringospira* has several unusual features of interest, chiefly in the pedicle valve. These center about the dental plates and the umbonal chambers.

Dental plates.—The dental plates are divergent toward the floor of the valve and meet the floor only for a distance of 3-4 mm. from the beak. They then are extended toward the brachial valve as sharp, tapering triangular plates which culminate in the teeth.

Teeth.—The teeth or articulating processes are small, slender points located at the angle between the hinge-margin and the delthyrial edge. The growth track of the tooth forms a squarish, thin rod along the delthyrial edge.

Umbonal chambers.—In most specimens of *Syringospira* observed by the writer the umbonal and delthyrial cavities are filled by blister-like plates of irregular form. These are laid down in almost any part of the shell, including the brachial valve. Deposi-

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EXPLANATION OF PLATE 36

Syringospira prima Kindle. All specimens from Percha formation (Box member), New Mexico. (p. 325)

FIGS. *1, 2*—Anterior view of a medium-sized and nearly complete individual showing the frill extending laterally from the palintrope, respectively ×1, ×2. Hypotype USNM 123370a. Hairpin bend at Georgetown, Silver City Quadrangle.

3—Side view of a complete specimen showing the wedge shape, ×1. Hypotype USNM 123359a. Bear Mountain, 6–7 miles northwest of Silver City.

4—Another specimen shown from the side to exhibit the roughened border where the frill has been broken away, ×1. Hypotype USNM 123368a. NE ¼ SW ¼ section 20, T. 17 S., R. 11 W., 4 miles east of Santa Rita.

5—Pedicle valve showing a nearly perfect frill seen from the anterior side, ×2. Hypotype USNM 123361a. Note truncated sides. Hairpin bend at Georgetown, Silver City Quadrangle.

6—View of the interarea of a small specimen, ×2, showing continuity of the frill with body of shell. The slight diagonal crack about 20 mm. from the left side marks the line between shell body and frill. Hypotype USNM 123359b. Bear Mountain, 6–7 miles northwest of Silver City.

7—View of the interarea of a small specimen, ×2, showing the elevated vertical lines and the cancellation of same by horizontal growth lines. On the left side the palintrope has been weathered away thus revealing the irregular sutures of the blister-like plates underneath. Hypotype USNM 123366a. Four miles east and ¼ to ½ mile north of Santa Rita.

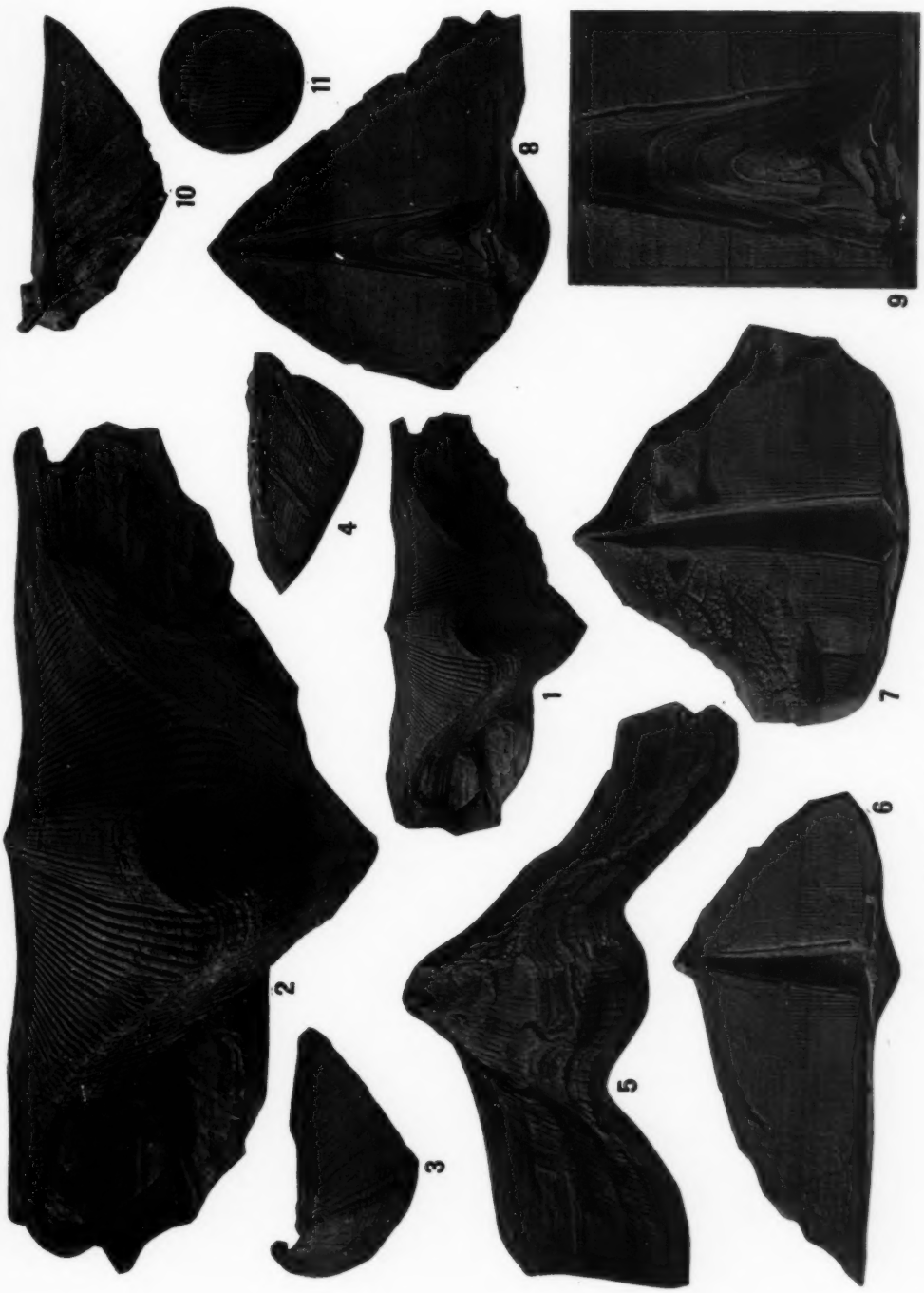
11—View of the interarea of an adult specimen, ×2, showing the fine vertical lines. Hypotype USNM 123364. Hairpin bend at Georgetown, Silver City Quadrangle.

Sphenospira alta (Hall). Chagrin shale (8 to 20 feet below the Cleveland shale), Chippewa Creek, one mile east of Brecksville, Cuyahoga County, Ohio. (p. 330)

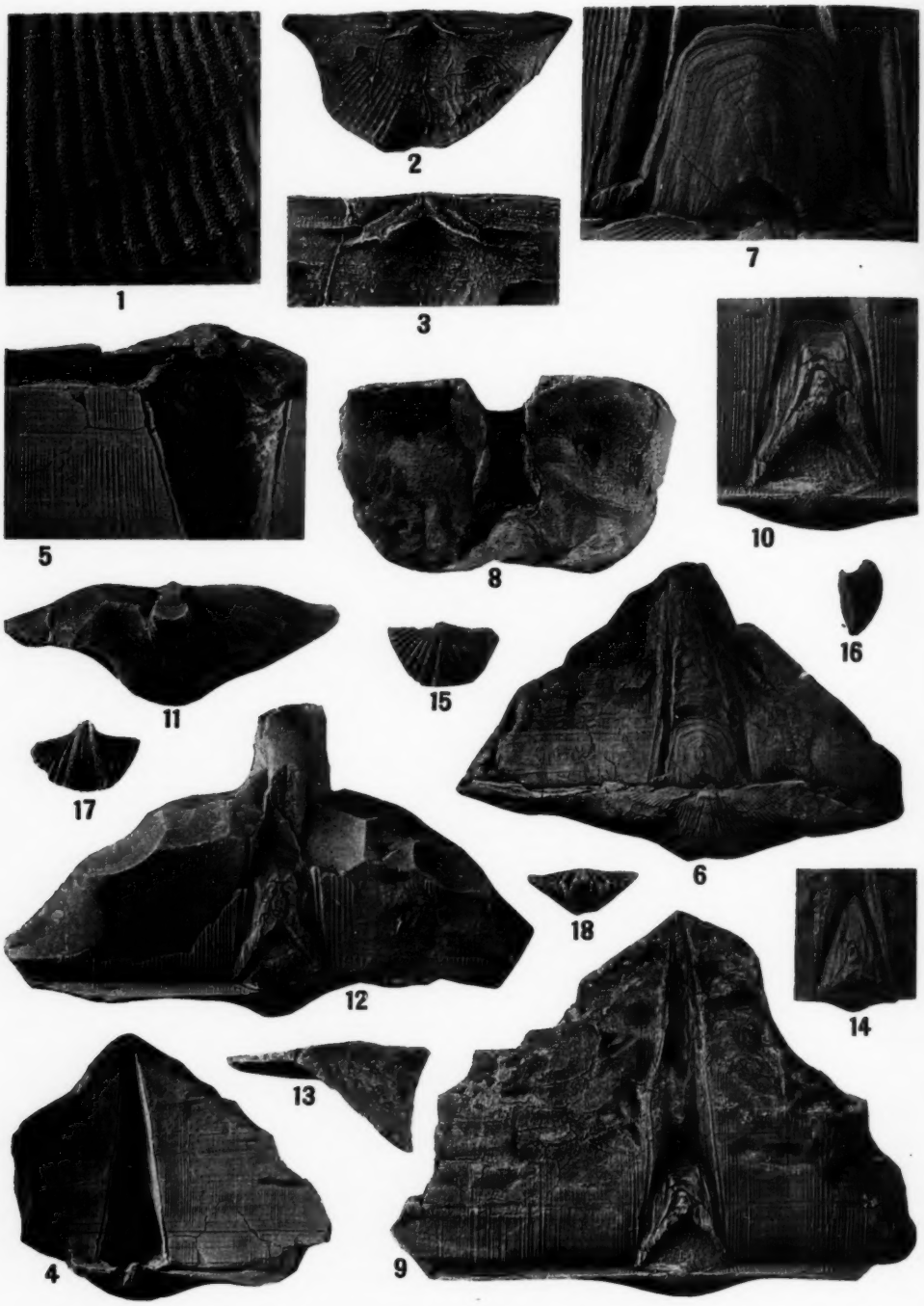
FIGS. *8*—View of interarea of a large and well-preserved specimen showing vertical striations, transverse delthyrial plate and stegidium. ×1. Hypotype USNM 123371a. Note remnant of frill on right side.

9—Enlargement, ×3, of the same specimen showing the stegidium in detail.

10—Side view of the same specimen showing the wedge shape and remnant of the frill, ×1.



Cooper, Unusual Devonian brachiopods



Cooper, Unusual Devonian brachiopods

tion of them starts in the posterior. The blisters fill the umbonal cavities and are deposited, without any apparent regularity on the floor and under the palintrope. When the shell is weathered these blisters form points of weakness so that a specimen may fall to pieces progressively from the pedicle beak toward the brachial valve. The blisters may also fall out of the palintrope and leave deep scoops as though a piece had been removed by the twist of a spoon. The extension of the palintrope and anterior shell is also sealed off by blisters which form a line of weakness along the lateral margins of the shell body. This is the reason why so few specimens are ever found with the palintrope frill or parts of it in place. The blisters on the inside edge make a line of weakness and the frill falls off as soon as the specimen is freed from the shale. The broken edge shows numerous small scoops where the blisters grew along the margin (text figs. 1, 2, 4; pl. 36, fig. 7; pl. 37, figs. 8, 11, 12).

These blisters form also in the delthyrial cavity and are built up from the valve floor

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EXPLANATION OF PLATE 37

Syringospira prima Kindle. All specimens from Percha formation (Box member), New Mexico. (p. 325)

FIG. *1*—Exterior of the brachial valve, ×5, showing the fine, elongate granules on the exterior. Hypotype USNM 123368a. NE ¼ SW ¼ section 20, T. 17 S., R. 11 W., 4 miles east of Santa Rita.

2, 3—Respectively ×1 of the brachial interior and ×2 of the cardinalia of the same specimen, a plasticine squeeze of an impression of the interior. The cardinal process and sockets are well shown but only the posterior part of the hinge-plates is visible. Hypotype USNM 123365a. Fork of Percha Creek, center north line section 16, T. 16 S., R. 8 W., on New Mexico highway 180, 2 miles east of Kingston.

4—Posterior view of an imperfect specimen showing the interarea, delthyrium and transverse delthyrial plate. The concave distal end of this plate is visible, ×1. Hypotype USNM 123359a. Bear Mountain, 6–7 miles northwest of Silver City.

5—Posterior view of the same specimen as shown in preceding, showing the interarea of the brachial valve with its vertical lines and the broad hinge-plate on the right side, ×2.

6—View of the interarea of a large specimen, ×1, showing stegidium. Hypotype USNM 123358. Northwest slope of Bear Mountain, about SW ¼ NW ¼ section 11, T. 17, S., R. 15 W., Grant County.

7—Enlargement of the stegidium of the preceding specimen, ×3, showing the concentric layers of growth. The deep grooves on each side are left by the removal of the tooth-rod from its socket on the edge of the delthyrium. The hole at the broad end does not mark the foramen but is a break in the otherwise complete stegidium. The broken piece is visible at the bottom of the hole.

8—Posterior part of a pedicle valve broken from the remainder of the shell and showing the blister-like plates which form planes of weakness, ×2. Hypotype USNM 123359c. Bear Mountain, 6–7 miles northwest of Silver City.

9—View of the interarea of a small specimen, ×2, showing vertical lines, delthyrium, transverse delthyrial plate, stegidium in place, and irregularities of the surface produced by pressure on the underlying blisters. Hypotype USNM 123366b. Four miles east of Santa Rita.

10—Enlargement, ×2, of the stegidium of the preceding specimen showing its incomplete nature and concentric layers.

11—Apical view of a specimen from which the apex has been broken showing the plug left by matrix filling the delthyrial cavity and the scalloped surface produced by exfoliation of the blister-like plates, ×1. Hypotype USNM 123363a. Bear Mountain road, 5.4 miles north of the junction of Atlantic and Alabama Streets, Silver City.

12—View of the posterior of another exfoliated specimen showing the plug (tube) left by matrix filling the delthyrial cavity, the stegidium and the scalloped scars of the blisters, ×2. Hypotype USNM 123367. Four miles east of Santa Rita.

13—Fragment of shell showing palintrope frill on left side and part of body wall, ×1. Hypotype USNM 123365b. Fork of Percha Creek, center north line of section 16, T. 16 S., R. 8 W., on New Mexico highway 180, 2 miles east of Kingston.

14—View of a small specimen showing stegidium having an acute apex, ×1. Hypotype USNM 123369a. Middle fork of Percha Creek, NE ¼ section 13, T. 16 S., R. 9 W., 1 mile west of Kingston, Hillsboro Quadrangle.

15–18—Respectively brachial, side, pedicle and anterior views of an immature specimen, ×2, showing erect beak and coarse granules on exterior. Hypotype USNM 123362. Center ½ section 13, T. 17 S., R. 15 W., 1 mile southwest of Bear Mountain, Grant County.

to join those of the delthyrial cavity. The blisters of the delthyrial cavity are separated from those of the umbonal chamber by the dental plates. This creates the illusion that there is a pedicle tube. No pedicle tube is present because the pedicle apparently migrated toward the brachial valve as the transverse delthyrial plate grew and as blisters were laid down anteriorly from the apex. The transverse delthyrial plate, the dental plates and the blisters between the dental plates and the valve floor define a cavity that forms a plug when filled with matrix. The plug is often undulating on its margins from scars of blisters. The plug protrudes when the blisters of the umbonal cavities are broken away. The plug or rod is the matrix filling the part of the delthyrial cavity not occupied by blisters. It is to this cavity which Stainbrook alludes when he mentions the pear-shaped delthyrial tube of *Syringospira*, which in reality is not a tube (text fig. 1; pl. 37, figs. 11, 12).

Brachial valve.—The same kind of blisters as those in the pedicle valve appear in various places inside the brachial valve, chiefly in the depression that corresponds to the fold. None of the specimens in the National Collection show any great thickening due to the blisters but these structures were only seen in the brachial valves of some small specimens. The largest specimens are not exfoliated on the brachial valve and therefore the blisters, if present, are concealed. The cardinal extremities of the brachial valve are drawn out into long, slender points which are in contact with the hinge edge of the palintrope frill.

The interarea of the brachial valve has already been mentioned. It is usually striated and the elevated lines bounding the striae appear opposite those of the pedicle interarea. The notothyrium is open in all specimens in which it could be observed. It permits examination of the socket plates even in specimens preserving both valves in contact. These form slightly concave triangles, the hypotenuse of which forms the edge facing the middle of the valve. The leg of the triangle away from the pedicle valve is thickened to form the inner wall of the socket. The socket is small but its growth track forms a long, oblique slit. Outside the slit is a low, narrow ridge, forming a minute accessory tooth that articulates with a fossette in the tooth of the pedicle valve. The leg of the triangle toward the pedicle valve meets the hypotenuse and is drawn out into the descending lamella to which the spire is attached.

The cardinal process is a more or less thickened boss with a small median, longitudinal depression and with its myophore face marked by thin, vertical plates as in many other spiriferoids. A complete spire was not seen but indications of it appear in several specimens. It appears to have been a broad-ribboned, oblique cone tapering into the lateral chambers of the pedicle valve (pl. 37, figs. 2, 3).

Types.—Figured hypotypes: USNM 123358, 123359a–c, 123361a, b, 123362, 123363a, c, 123364, 123365a–c, 123366a, b, 123367, 123368a, c, 123369a, 123370a; unfigured paratypes: USNM 123360, 123363b, 123365d, 123368b, d, 123369b, 123370b.

Horizon and locality.—Percha shale (Box member), vicinity of Silver City, Santa Rita, Georgetown and Kingston, New Mexico. Detailed localities are given in the plate legends.

Genus SPHENOSPIRA Cooper, n. gen.

Plate 36, figures 8–10; text figure 5

Type species.—*Spirifera alta* Hall, 1867, Palaeontology New York, vol. 4, p. 248, pl. 43, figs. 2–8 (fig. 1 is probably the impression of the brachial valve of *Cyrtospirifer* or *Cyrtiopsis* and is therefore excluded from the species).

Exterior.—The exterior of the new genus here proposed for "*Cyrtia*" *alta* is nearly identical to *Syringospira*. It has the same wedge-shaped profile, the semi-conical pedicle valve, and the shallow brachial valve. None of the impressions of the interarea available for study shows the vertical lines clearly but they are there in patches nevertheless. Although most of the exterior impressions are badly worn, one of them shows a trace of the granules on the exterior.

Although the exterior of *Syringospira* and *Sphenospira* are nearly identical, one important difference does exist. *Sphenospira* is not provided with the prominent frill that is built out from the interarea as in *Syringo-*

spira. Of all the specimens of *Sphenospira* examined a few exhibit a small flap at the cardinal extremities of the pedicle valve. This is best shown in a specimen from the Chagrin shale of Ohio, USNM 123371a. The frill appears about 12 mm. away from the hinge-line and about 30 mm. along the shell margin from the beak. This narrow frill when produced to its probable limits (text fig. 5) would have been about 20 mm. long. This would be an addition to the width of the shell-body of the specimen which is about 60 mm. wide, to produce a total width of about 100 mm. The frill of *Sphenospira* thus does not originate at the beak like that of *Syringospira* and is thus not nearly so elaborate. Indications on the brachial valve are that a long point extended from the cardinal extremity and ran along the frill to its end (text fig. 5; pl. 36, fig. 8).

The delthyrial cavity is covered by a long transverse delthyrial plate exactly like that of *Syringospira*. The gape between this plate and the brachial valve is covered by a stegidium like that of the Percha genus (pl. 36, figs. 8, 9).

Interior.—The interior of *Sphenospira* has some important differences from that of *Syringospira* but the major structures are the same. The dental plates of *Sphenospira*, unlike those of *Syringospira* are long and divergent, extending toward the brachial valve for at least 10 to 22 mm. depending on the size of the animal. The muscle scars are well exhibited between the dental plates in impressions of the interior, and show the radiating ridges familiar in spiriferoids. No evidence of blisters was seen in the interior impressions of any specimen of *Sphenospira* studied, nor was any evidence of them seen in any published figures of that genus.

The interior of the brachial valve of *Sphenospira* is essentially the same as that of *Syringospira*. The cardinal process has a wider and deeper median pit and the hinge-plates are more robust than those of *Syringospira* but these may be only size or ecological differences.

Types.—Figured hypotype: USNM 123371a; unfigured hypotype: USNM 123371b.

Horizon and locality.—Conewango stage, New York and Pennsylvania. Detailed locality given in plate legend.

Discussion.—The generic distinction between *Syringospira* and *Sphenospira* is thus the more elaborate frill development, lesser prominence of the dental plates and the development of the cysts on the interior of *Syringospira*. The presence of the cysts in that genus is not a sporadic development because they appear in all adults sectioned and all partly weathered ones. The frill of *Syringospira* is more elaborately and differently developed from that of *Sphenospira*. The Ohio specimen studied is more conspicuous in this respect than any New York or Pennsylvania specimens studied.

Hall realized that his species *Spirifera alta* was unusual in the great development of the transverse delthyrial plate that partially closes the delthyrial cavity. He stated (1867, p. 248) that the "margins of the fissure [delthyrium] are grooved, as in other species for the reception of a pseudo-deltidium." The groove referred to is probably the one formed in the breaking out of the rod produced by the growth of the tooth. Hall did not mention, nor did he figure, the stegidium that covers the gape between the distal end of the transverse delthyrial plate and the brachial valve although impressions of this plate are visible in New York and Pennsylvania specimens.

Syringospira and its homeomorph *Sphenospira* are closely related to other Devonian and Mississippian genera. *Eosyringothyris* is a related Middle Devonian genus which is characterized by a pustulose exterior, broad palintrope and prominent dental plates. This genus also possesses a transverse delthyrial plate in the delthyrial cavity like that of *Syringospira* and *Sphenospira* although the one in *Eosyringothyris* is not so elaborately developed. *Pseudosyrinx* is a related form which has a surface ornamentation consisting of minute pustules or hair-like spines, wedge-shaped profile and a broadly triangular interarea. It also possesses a long transverse delthyrial plate like that in *Syringospira* but no stegidium has yet been seen in *Pseudosyrinx*. This genus differs from *Syringospira* and *Sphenospira* in having a smooth fold and sulcus on the exterior.

Comparison with *Syringothyris* cannot be made because that genus possesses a punctate shell and a syrinx neither of which are

developed by the genera under consideration or *Eosyringothyris* or *Pseudosyrinx*.

LIFE HABITS

Inasmuch as the exteriors of *Syringospira* and *Sphenospira* are so close it can be assumed safely that their life habits must have been the same. The discussion therefore, which is based on *Syringospira* will serve for the other genus as well. Furthermore the two genera lived on fine sands or coarse muds and their form is adapted to keep them on the muddy or sandy surface which may have been moderately firm. All specimens of *Syringospira* observed in place on the outcrop, especially in the exposure on New Mexico Highway 180, 2 miles east of Kingston, were lying on the broad face of the palintrope, the interarea. This is undoubtedly the actual position of the animal in life. The wedge shape, the large and wide frills are advantageous in helping the specimen to lie on the bottom. The perpendicular corrugations of the interarea, it is believed, would be helpful in preventing the individual from being moved sideways by bottom currents. It is believed that the animal lived with interarea of its shell down and the sharp edge of the wedge or apex of the pedicle valve facing the current direction. Water currents would slip over the sloping wedge without moving it. At first the shell was anchored by a pedicle but in later life this was pinched off by growth of the stegidium and the animal lived anchored only by its weight on the broad surface of the palintrope.

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FORM-GENERA IN PALEONTOLOGY

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ABSTRACT—It is suggested that, whereas no legal objection exists to the establishment of form-genera according to the present Rules of Nomenclature, the present procedure of naming conodonts, if allowed to continue unregulated, will lead to ambiguity. The opinion of further paleontologists is sought before any formal proposals are made to the International Commission.

INTRODUCTION

THE recent notes by Sinclair (1953) and Rhodes (1953a) have drawn attention to the longstanding problem of form-genera in paleontology. Rhodes (1952, 1953a, 1953b) has adopted the dual nomenclatural procedure first advocated by Scott (1942) for describing respectively (a) disjunct conodont remains, and (b) their natural assemblages. Sinclair rightly points out that the logical application of the Rules of Nomenclature to this situation leads to the suppression (as junior synonyms) of most if not all of the names introduced for such natural assemblages in favor of the earliest names of one of the constituent members of each assemblage. This course would naturally play havoc with the nomenclature at present in vogue for the disjunct remains, so that an entirely new system would have to be introduced for them, such as Sinclair's suggestion of using the phrase "the subbryantod element of *Streptognathodus elegantulus*" instead of the name "*Ozarkodina delicatula*." Rhodes (1953a) believes the adoption of this suggestion of Sinclair's to be impracticable. But Sinclair also suggested that the problems raised might be such that the International Commission should be asked for some sort of special dispensation in the Rules. It is the purpose of the present note to examine further the desirability of this latter suggestion.

LEGAL POSITION OF THE PRESENT PROCEDURE

Junior synonyms, according to the Rules, can only be finally rejected as invalid if they are *objectively* synonymous; i.e., if they are based on the same type material as the senior rival. Otherwise they are *subjective* synonyms and can always be validly used by a taxonomist who disagrees with the synonymy. So long, then, as a specific name introduced for a conodont assemblage is not based on the same type specimen as one of its constituent form-species, and so long as a genus proposed for a conodont assemblage is not based on the same species as a form-genus, they cannot be classed as objective synonyms. Consequently there is no *legal* objection to the concurrent use of the two alternative systems of nomenclature.

So far as I know, no name specially proposed for an assemblage has ever been based on anything other than an assemblage presumed by its author to be natural. Nor, from the nature of the case, is it ever likely to be based on anything else in the future. Therefore assemblages are not based on disjunct remains. It is however possible that disjunct names might be given to the constituents of an assemblage. It remains to consider whether such a course is desirable or not.

DESIRABILITY OF THE PRESENT PROCEDURE

Some zoologists may feel that although the dual system of nomenclature may be legal, it is nevertheless undesirable in that it contravenes a principle of nomenclature—that a species should have only one name. Although this principle is not stated as a mandatory provision of the code, and indeed, is not at present stated at all, it was recommended at Copenhagen that some such concept should be incorporated in a general preamble to the Rules.

However, the Rules are not designed to trespass on the freedom of taxonomists to classify animals in any way they wish, and it seems probable that some (perhaps most) conodont specialists would prefer to be allowed to continue their present procedure.

It is important that the consequences of whatever course is taken should be fully understood. The present system of nomenclature has been energetically applied to the discrete parts of conodonts for the last twenty-seven years—ever since the publication of Ulrich and Bassler's classification (1926). During these years at least 112 generic and over 1500 specific names have been proposed for conodonts. Many of these are certainly synonyms, but such figures nevertheless give some indication of the size and scope of the taxonomic problem involved. Contrast with these figures the five generic and six specific names that have been proposed for assemblages, and you gain an idea of the extreme abundance of conodonts on the one hand, and the rarity of assemblages on the other. There seems no likelihood that it will ever be possible to assign more than a very small minority of conodonts to an assemblage, and it will only be possible to employ Sinclair's "subbryantod element" system in this small minority of cases. For all the rest we must either continue to use the present system, or invent an entirely new system of cyphers or figures, or, perhaps, turn to the "military classification" of Croneis (1938), which (as Dr. Sinclair has pointed out to me) was outlawed for the purposes of zoological nomenclature by the International Congress at Paris in 1948. However much the general taxonomist may wish that such a system had been adopted thirty years ago, it now seems unrealistic to suggest that it should be enforced by rule on our colleagues. In the writer's view, such a course would be a flagrant violation of the principle of "no interference with taxonomic freedom"—a principle also to be incorporated in the preamble to the new Rules. It therefore seems essential to the present writer to ensure that it remains possible:

(a) to continue admitting two systems of nomenclature, one for assemblages and one for disjunct remains; and
(b) to give a name to any taxon in either group which cannot be confused with another taxon in either its own or the other group.

If this is to be attained, it is clearly necessary to avoid using the same name in more than one group. Now, though the Scott-Rhodes system is legal, and though it avoids the ambiguities suggested in (b) above, it remains true that Sinclair's alternative system (his first suggestion) remains legal also, and, indeed, it was adopted by Schmidt in 1934. There would clearly be considerable danger of confusion if both systems were to be used indiscriminately. For, if assemblages are named with the oldest available name of one of their constituent parts, and the same name retained for the element itself when there is no evidence to which assemblage it belongs, we shall be in the unsatisfactory position of having one name applied to two concepts. Moreover, there would be a lack of universal usage which would contravene a third principle of nomenclature that is to be incorporated in the preamble of the new Rules. It seems necessary, therefore, to outlaw one of the two systems, and that can only be achieved by modification of the present Rules.

PROCEDURE IN PALEOBOTANY

Although the problem has arisen in the present case as a result of the study of conodonts and scolecodonts, it is not new to paleontology, for an exactly similar situation occurs in the study of the disjunct remains of fossil plants. The solution in paleobotany has been to introduce an appendix to the Code dealing with "special provisions concerning fossil plants." These provisions admit and define "organ-genera" and "form-genera." The definition of the latter given in the new "International Code of Botanical Nomenclature" (Lanjouw, 1952, p. 64) is as follows:

> A form-genus is one that is maintained for classifying fossil specimens that lack diagnostic characteristics indicative of natural affinity but which for practical reasons need to be provided with binary names. Form-genera are artificial in varying degree.

RECOMMENDATIONS

In the present author's opinion it is undesirable to create rules for paleozoologists which differ from those for neozoologists. No suggestion is therefore made for the adoption of the botanical solution verbatim. Some such provision for the creation of form-genera and form-species would seem however to be definitely desirable, and, if introduced, could apply equally to neo-

zoology. However, this is not to suggest that any case is in view in which such a scheme could be recommended for the classification of parts of recent animals.

One complication, foreseen by Dr. Sinclair, needs to be mentioned. Nobody is certain of the zoological affinities of the conodonts. It is conceivable that names given to conodont assemblages might themselves be considered "form-genera," consisting, as they do, of parts of unknown animals. Such a case is even more likely in the scolecodonts, which are known to be the remains of annelids. There is no reason why provisions for the establishment of form-genera could not admit one class of form-genera within another, though it would not seem advisable to the present author to regard either conodont or scolecodont assemblages as such.

This is not the place to put forward concrete proposals for the alteration of the Rules of Nomenclature. It is suggested however that such proposals should in due course be submitted to the *Bulletin of Zoological Nomenclature*. In the meantime it would be interesting to learn the opinions of other paleontologists, for there may perhaps be a compromise solution which has escaped both Dr. Sinclair and myself.

THE SPECIES CONCEPT IN PALEONTOLOGY

In conclusion it may be pointed out that, if the observations in this note were accepted, the word "species" would be used in paleontology to cover three rather different concepts:

(a) *"true" species;* i.e. the so-called "Linnean" species of Eagar (1949, p. 272) and George (1953), which are taxa based on the population concept and therefore equivalent to the species of the neozoologist;

(b) *morphological species* (see Eagar and George, op. cit.); taxa based on individuals of stated morphological character. Several morphological species may be contained within one true species. For example, Spath (1938, p. 25) has stated that an assemblage from one bed divided by him into seven species and seven varieties of the ammonite genus *Beaniceras* "formed one interbreeding population." Again, Hudson and Fox (1943) place 94 specimens of rugose corals from a 3-ft. band of shale in a "species-group" which they divide up into seven species, relegated to four genera. They state that these specimens can be divided into two distinct groups, each including "one or more plexus sections composed of forms linked by intermediate varieties." The species-plexus, they say, "is, in a phylogenetic classification, the equivalent of a species." The present author has elsewhere (Sylvester-Bradley, 1951) suggested that such morphological species can more conveniently be regarded as varieties of a true species. Such a course would affect nomenclature only to the extent of adding the prefix "var." to the so-called "specific" name, and would remove a cause of confusion between paleontologist and neontologist.

I have previously (Sylvester-Bradley, 1951, p. 101) stated that if the Paris decisions of the International Commission were to be ratified, the Rules would demand that such varietal names should be relegated to a new category: "infra-subspecific form." At the Congress held in Copenhagen in 1953 special provision was made to exempt the variety (as used in this sense in paleontology) from the Paris ruling, so that such a varietal name may, in the future as in the past, still be regarded as nomenclaturally co-ordinate with the species. There seems, therefore, to be no reason why the variety cannot be quoted as a *binomen* where necessary, thus removing the objection raised, on the grounds of clumsiness, by Hudson and Fox.

(c) *form species*, which would be taxa within form-genera and themselves could either be based on populations (and therefore be "true" form-species) or on individual "morphotypes" (George, 1953) when they would be morphological form-species. Thus Rhodes (1953b), in a paper describing form-species of conodonts, states that "varieties . . . are understood to be distinctive types of individuals within a 'population' (in so far as this term can be applied to a group of conodonts)." Rhodes' form-species are therefore "true," the variety taking the place of the morphological form-species.

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THE EOCENE MAMMALS FROM THE LYSITE MEMBER, WIND RIVER FORMATION OF WYOMING

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ABSTRACT—Revision of the mammals from the type area of the lower Eocene Lysite is possible on the basis of three collections in the Amherst Museum. Additions to the known fauna include the rodent, *Leptotomus;* the creodonts *Thryptacodon, Anacodon* and *Prolimnocyon;* the uintathere, *Probathyopsis;* the pantodont, *Coryphodon;* and the artiodactyl, *Diacodexis*. Sufficient material is at hand to permit a statistical analysis of two genera, *Hyopsodus* and *Hyracotherium*, which shows that the morphologic characters heretofore used to characterize species are generally individual variants, and that not more than three species of *Hyopsodus* and two of *Hyracotherium* are present. Two new species are described: *Thryptacodon loisi* and *Probathyopsis lysitensis*.

INTRODUCTION

A RELATIVELY large number of specimens of fossil mammals of the Lysite member of the Wind River formation (upper lower Eocene) of Wyoming is available at the Amherst College Museum. This material consists of three collections, made by Loomis in 1904, Wood in 1948 and Kelley in 1951, totaling 465 identifiable mammal specimens. That of Kelley is the largest, containing about 270 specimens. Although the material is all fragmentary, and much is merely isolated teeth, it is adequate to warrant a revision of the fauna as a whole. Since the Wind River Lysite is part of the standard sequence of the North American continental Tertiary, the restudy of its fauna is of particular importance.

The authors wish to express their appreciation to Dr. David Kitts who has allowed us to use his conclusions as to the correct names to be applied to the Lysite horses.

This paper deals largely with material from the type locality of the Lysite, an area approximately 4 miles long and 1 mile wide along the eastern boundary of the drainage basin of Cottonwood Creek, north of the town of Lysite, Fremont County, Wyoming. Much of Loomis' material is from Bridger Creek, about three miles farther west. No significant additions to the geology of the locality can be given beyond what is included in Granger (1910) and Tourtelot (1946).

The fossils are found at all levels, Granger (1910, p. 245) stating that they "are particularly abundant near the base, especially in a dark red sandy shale stratum." The authors, however, have found that fossils were almost restricted to the upper 60 feet of exposures, and particularly abundant in the top 30 feet. Turtle and crocodile scrap are found almost everywhere and at most levels, but are usually associated with red gravelly sandstones. Fragments of *Coryphodon* are occasionally found with these forms, but other mammals are very rare. Most of the collections were made either in beds of mottled purple, red and white, or in fine white sandstones. A number of pockets were found, with numerous jaws and jaw fragments, occupying an area of 3 or 4 square yards. These were generally in the white sandstones.

The mammalian fauna includes the following forms, represented at Amherst by the numbers of individuals indicated:—

Insectivora	
Cynodontomys latidens	24
Tillodontia	
**Esthonyx bisulcatus*	5
Primates	
Absarokius abbotti	7
Omomys minutus	1
Pelycodus sp.	8
Phenacolemur sp.	1
Rodentia	
Paramys major	12
P. bicuspis	10
P. excavatus	3

[1] This study was assisted by a grant from the Rockefeller Foundation.

**Leptotomus* n. sp.	1
"Sciuravus" depressus	10
Carnivora	
**Thryptacodon loisi* n. sp.	1
**Anacodon ursidens*	1
**Oxyaena ultima*	4
**Prolimnocyon elisabethae*	1
Didymictis altidens lysitensis	7
Condylarthra	
**Phenacodus primaevus*	2
P. copei	6
P. vortmani	2
P. brachypternus	1
Hyopsodus mentalis	54
H. powellianus	71
H. minor	1
Dinocerata	
**Probathyopsis lysitensis* n. sp.	2
Pantodonta	
**Coryphodon* sp.	23
Perissodactyla	
**Hyracotherium vasacciense*	96
H. craspedotum	24
Heptodon ventorum	14
Artiodactyla	
**Wasatchia* cf. *W. dorseyana*	3
Bunophorus macropternus	4
**Diacodexis chacensis*	12

Of this faunal list, the twelve marked with an asterisk were not recorded by Van Houten (1945, Table IV) from the Wind River Lysite. Some of these (*Anacodon ursidens*, *Phenacodus primaevus*, *Coryphodon* sp. and *Diacodexis chacensis*) were previously known from the Lysite equivalent of the Big Horn Basin, so that their discovery in the Wind River Lysite is merely an extension of their geographic range. The identification of *Oxyaena ultima*, *Hyracotherium vasacciense*, and *Wasatchia dorseyana* is a matter of terminology only, and does not represent a significant addition to the fauna. *Esthonyx* sp. was listed by Van Houten from the Lysite, and this record is merely the identification of the species present. The other five forms, however, require a little comment. *Leptotomus* has previously not been recorded prior to the Bridger. The revision of the Paramyidae now being made by the junior author shows that this genus (with a still undescribed species) is found in the Lysite. *Thryptacodon* was not recorded by Van Houten later than Gray Bull. Gazin, however, has described it from the lower Lost Cabin level of the Knight, so it is a reasonable addition to the Lysite fauna. *Prolimnocyon* ranges through the lower Eocene, although it previously was not certainly identified in any Lysite equivalent. The Lysite specimen seems identical with *P. elisabethae*, from the lower Lost Cabin level of the Knight. There has been a surprising gap in the known history of the uintatheres, with none known from any of the Lysite equivalents. While it is not surprising that one should have been found, *Probathyopsis lysitensis* helps to fill in the sequence of these forms.

A statistical investigation of the species of *Hyopsodus* and *Hyracotherium* resulted in the following generalizations:

a. the collections are a random sample of animals buried in the deposits and therefore may be presumed to be a random selection of the original population;

b. it is obvious that a holotype is only the one particular member of a population which happened to be first described, not necessarily being a representative of the mean of the population, and sometimes even being an extreme;

c. the specimens representing the two genera are variable in both size and morphology, so that some specimens could not with certainty be placed in any one of two or more previously described species;

d. since there seem to have been relatively few species or subspecies living in the small Lysite area during the brief period involved, several forms must be synonyms.

The study of these two genera was an attempt to determine the species boundaries and not to compare probable species variability as is the case in neontological population studies. Since no population studies have been made on lower Eocene mammals, no population comparisons could be made. Indeed, it was difficult to determine what statistical methods to employ. Although means, deviations, etc. were computed, they have intentionally been omitted in the discussion because:

a. there is no certainty that the specimens in the Amherst Museum represent all, or even most, of the variations within the Lysite population;

b. in the case of some isolated teeth it was difficult to determine whether it was a first or second molar; and

c. it was generally impossible to correlate variations in lower teeth with those in upper teeth, due to the fragmentary nature of the specimens.

Comparative regression lines and many of the graphical methods of determining

population trends were found to show nothing. The statistical treatment of these two groups is preliminary and not meant to be comprehensive since it was based only on material at Amherst.

SYSTEMATIC DESCRIPTIONS

Order INSECTIVORA

Family MIXODECTIDAE

CYNODONTOMYS LATIDENS Cope, 1882

Figure 2, A–E

There are 24 specimens of this genus, all specifically identifiable.

Only one species, *C. latidens*, has been identified from the Lysite. *C. angustidens* is characteristic of the Gray Bull and *C. scottianus* of the Lost Cabin. Matthew states that these three species "appear to be in genetic sequence, the stage of progress of each specimen being in exact correspondence with its recorded geological level" (1915c, p. 471). He then gives the following key:

1. *C. angustidens* sp. nov. P_4–m_3=14 mm. P_4 narrower, oval, with small heel and deuteroconid much smaller than protoconid.
2. *C. latidens* Cope. P_4–m_3=15 mm. P_4 with deuteroconid distinctly smaller than protoconid, heel narrower than in *C. scottianus*, its cusp less separate.
3. *C. scottianus* (Cope). P_4–m_3=17.3 mm. P_4 with deuteroconid a little smaller than protoconid, and heel broad basined with hypoconid and entoconid wide apart.

Using Matthew's key, all the Amherst Lysite material seems to be intermediate between *C. angustidens* and *C. latidens*. From Matthew's definition it is almost impossible to determine what structural differences exist between these two species. For example, there is no clear difference between "deuteroconid much smaller than protoconid" and "deuteroconid distinctly smaller than protoconid," or between "small heel" and "heel narrower than in *C. scottianus*."

The following additional minor distinctions have been noted:

C. angustidens	*C. latidens*
P^4 no conules	faint conules
M^1 no mesostyle	"rudimentary" mesostyle
P_4 entoconid faint, not separated from hypolophid, hypoconid crested	entoconid moderately developed and moderately separated from hypolophid, hypoconid less crested and more tubercular
M_3 heel less elongate, hypoconulid less isolated	heel elongate, hypoconulid isolated

These structural differences, like those given by Matthew, are merely relative increase of prominence and development of certain structures, *C. latidens* consistently being more advanced. The structural differences between these forms are exceptionally minor, similar to some that are found to exist within the single species populations of other Lysite genera.

These structural differences do not seem to be significant of specific differences. There is only a 1 mm. difference between the total P_4-M_3 measurements of the two species. Even considering the size of the animals, this does not seem to be an effective specific difference. These two species apparently represent the end extremes of the same population extending from Gray Bull to Lysite and it would be expected that intermediates would be found that would tie the two species into a continuous inseparable series.

There were enough specimens of the genus in the Amherst collections to determine a range and mean of measurement of each lower tooth from P_4 to M_3. Population curves based on length of each tooth give a characteristic continuous monomodal curve, indicating a single population during the Lysite (fig. 1). Comparison of the ranges, means, and distribution curves for length of each tooth with the measurements of the holotypes of the two species reveals that the population is generally closer to the holotype of *C. angustidens* than to that of *C. latidens*. The same is true of width and proportions of the teeth. Therefore, the population could be better identified as *C. angustidens* than *C. latidens*, if the two are considered to be distinct.

In minor structural differences between the two species brought out above, the Amherst specimens were again intermediate, and ran the entire range of variability from one type to the other. The metaconid of P_4 ranges from a low cusp, essentially part of the protoconid, to one subequal with the protoconid and widely separated from it

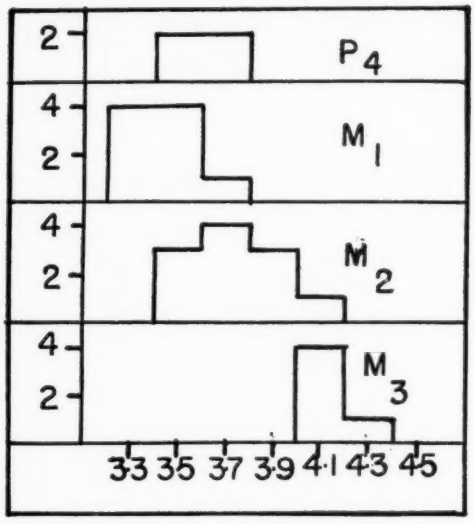

FIG. 1—Variation in tooth size of *Cynodontomys*. Ordinate = number of specimens, abscissa = tooth length in mm.

(fig. 2, A). The hypoconid of the same tooth ranges from a cone (fig. 2, A) to a blade (fig. 2, B). The paraconid may be invisible, a narrow ridge, or a cuspule. There is great variation in the size of the entoconid. M_1 is relatively small (fig. 2, C). All specimens of M_3 have a narrow, isolated hypoconulid (fig. 2, D). The greatest transverse width of all lower molars is across the talonid. The upper teeth are represented by a single specimen, so that nothing can be told of their variability. They are similar to those of the referred material, AMNH 15629, except for being somewhat smaller (fig. 2, E).

It is almost impossible to establish workable structural differences on such minor variations. Although arbitrary categories were made of each, there was found to be an integration of variations. For example, in two lower fourth premolars, Amherst 3477 and 10153, the entoconid is very slight or rudimentary and not separated from the hypolophid, which is a *C. angustidens* variation; however, the heel is moderate to broad, the hypoconid is tubercular, and the metaconid is moderately developed and moderately to well separated, all of which are characteristics of *C. latidens*.

Cynodontomys seems to have been increasing slowly in molarization and size from Gray Bull to Lysite and considerably faster from Lysite to Lost Cabin. The Amherst material is intermediate in all characters between the holotypes of *C. angustidens* and *C. latidens*. Matthew (1915c, fig. 46) figures a specimen from the upper Gray Bull also intermediate between the two species. None of the specimens included in this study could be considered as being intermediate between *C. latidens* and *C. scottianus*, or between *C. latidens* and *C. knightensis*. The latter (Gazin, 1952, p. 20) is clearly more advanced than the present material in the extensive molarization of P_4. There is then a continuous series of *Cynodontomys*, from Gray Bull to Lost Cabin, whose extremes are specifically separable. A division into Gray Bull and Lysite forms on one hand and Lost Cabin on the other fits the data better than Matthew's three species. The Gray Bull and Lysite forms are hence considered to be conspecific, and are referred to *C. latidens* as it has priority over *C. angustidens*.

As indicated by Matthew (1915c, p. 442), Loomis' species *Notharctus cingulatus* and *N. palmeri* are clearly *Cynodontomys latidens* and are merely extremes of a varying population including the other Amherst specimens referred to this species. The tooth Loomis identified as RP_4 in the holotype of *N. cingulatus* is LP_4.

Order TILLODONTIA
Family TILLOTHERIIDAE
ESTHONYX BISULCATUS Cope, 1874
Figure 3, A–B

Five specimens are referable to *Esthonyx*. The lower Eocene species have not been described since Cope's original descriptions. Van Houten lists (1945, p. 449) one or more undetermined species from the Lysite of both the Big Horn and Wind River Basins. *E. bisulcatus* Cope has been recorded as ranging from Clark Fork to Largo. *E. acutidens* Cope is known only from the Lost Cabin horizon of the Wind River and Knight Basins. The two other species of the genus, *E. latidens* Simpson and *E. grangeri* Simpson, are restricted to Clark Fork and lower Gray Bull. Denison records *E. bisulcatus* from the Wind River ?Gray Bull. The specimen differs from typical members of the species "only in the slightly smaller size and in the less strongly developed hypoconulid lobe of M_3" (1937, p. 14).

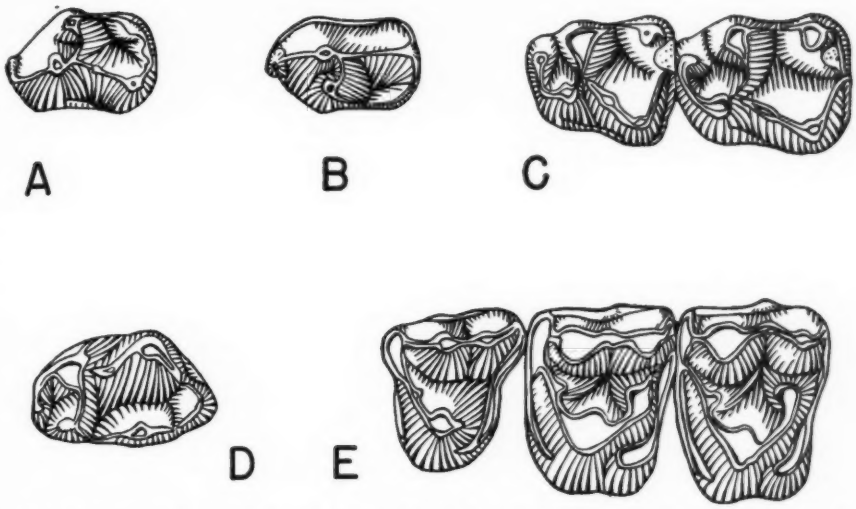

FIG. 2—*Cynodontomys latidens*, ×6. *A*, Amherst 3477, LP_4, holotype of *Notharctus cingulatus* Loomis; *B*, Amherst 329, RP_4, holotype of *N. palmeri* Loomis; *C*, Amherst 11035, LM_{1-2}; *D*, Amherst 10164, RM_3; *E*, Amherst 11253, LP^4–M^3.

Comparison of the Amherst material with *E.* ? *bisulcatus* from the Clark Fork, AMNH 16065 (Simpson 1937, fig. 1), and with the two specimens of *E. bisulcatus* figured by Cope (1877, pl. 40, figs. 27–31), shows that, although variations in proportions exist, they are not separable from *E. bisulcatus*, especially considering the large amount of variation mentioned by Simpson. The Amherst specimens are, however, probably smaller than the mean for the Big Horn Gray Bull population and may in size correspond to Denison's material from that horizon in the Wind River Basin.

Amherst 11233, 3301, and 3282 agree well morphologically with Cope's figures of *E. bisulcatus* (1885, pl. 24a, figs. 22–25; pl. 24c, figs. 1–10) although there are variations in size and proportions. The teeth increase in size from P_4 to M_2. P_4 is narrow, with a long trigonid and well separated paraconid and metaconid (fig. 3, A). On the other teeth the paraconid is more a swelling at the end of the protolophid. The metastylid on all teeth is moderately developed (fig. 3). The teeth become progressively larger as far as M_2, and the greatest transverse width of M_1 and M_2 is across the trigonid.

Amherst 3582 differs from the corresponding tooth in No. 11233 in the complete lack of a metastylid, and in proportions, but agrees well in all other characters.

Amherst 10124, a fragment of M^3, agrees quite well with the corresponding tooth of a maxillary fragment from the Gray Bull referred to *E. bisulcatus*, except in having a more elongated paracone.

Comparison with *E. acutidens* is practically impossible, since the only duplication between the type of this species and the teeth in the Amherst collections is an isolated tooth, either M_1 or M_2 (Cope, 1885, pl. 24a, fig. 21), probably the former. Whichever tooth it is, the Amherst material is smaller. A fragment of M^3 from the Lysite has the same elongated paracone shown by Cope (op. cit., fig. 18), but is smaller.

There seems to be no present basis for separating the Amherst Lysite specimens from *E. bisulcatus* in spite of variations in proportions and minor differences in structure. The antero-posterior measurements for P_4 fall within the range noted by Simpson, and the minor differences in pattern should easily permit the specimens to be included in this species.

Order PRIMATES
Family ANAPTOMORPHIDAE
Genus ABSAROKIUS Matthew, 1915

Matthew (1915c, p. 463–464) established the genus *Absarokius* with *Anaptomorphus abbotti* Loomis as the type species. He sepa-

rated the genus essentially on the following criteria:

Anaptomorphus
Dentition I_2 C_1 P_2 M_3
M_3 unreduced
Two minute incisors, small canine
P_4 smaller than M_1

Absarokius
Dentition I_1 C_1 P_3 M_3
M_3 reduced
One incisor and canine moderately large
P_4 larger than M_1

Absarokius also is very similar to *Tetonius*, especially in the construction of the molars. Matthew pointed out the close similarities of the cheek teeth, with those of *Absarokius* merely slight advances on those of *Tetonius homunculus*. But he showed that in the front teeth, *Absarokius* is more primitive, *Tetonius* having a single large tooth in front of the small P_2, while in *A. abbotti* there were two of moderate size. He considered the genera very closely related and raised the possibility that the only specimen of *A. abbotti* in which this area was preserved might be abnormal in these respects. The type specimen of *A. abbotti* (Amherst 3479), a beautifully preserved jaw fragment containing P_3–M_3, does not help in this most important generic character as the jaw fragment ends just anterior to P_3. In Amherst 11009, there is enough in front of P_4 to indicate the broken roots of P_3, a small alveolus for P_2, and in front of this there appears to be the

FIG. 3—*Esthonyx bisulcatus*, ×4. *A*, Amherst 11233, RP_4–M_1; *B*, Amherst 3301, RM_1.

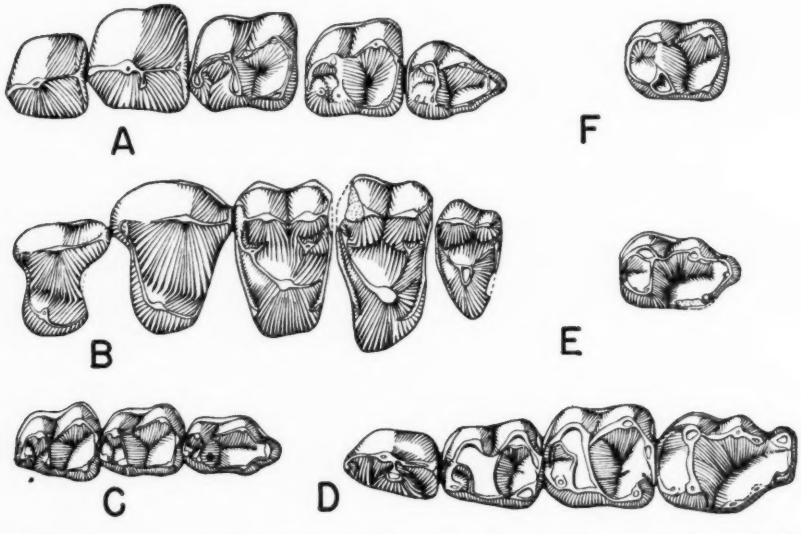

FIG. 4—Teeth of Primates, mostly ×6. *A*, *Absarokius abbotti*, holotype, Amherst 3479, RP_3–M_3; *B*, *A. abbotti*, Amherst, 10201, LP^2–M^3; *C*, *Omomys minutus*, holotype, Amherst 3365, RM_{1-2}; *D*, *Pelycodus* cf. *P. jarrovii*, Amherst 3542, RP_4–M_3, ×3; *E*, *P.* cf. *P. frugivorus*, Amherst 11173, RM_3, ×3; *F*, *Phenacolemur* sp., Amherst 3463, RM_2.

posterior portion of the alveolus of a small to moderate sized canine, indicating that this is a normal character. Gazin points out the same condition in *A. noctivagus* from the La Barge level of the Knight (1952, p. 24).

The only other differences between *Absarokius* and *Tetonius* are slight variations in proportion and structure, the most significant of which is that P_{3-4} are usually larger in *Absarokius*. This variation could certainly be considered intra-generic were it not for the difference in the anterior teeth.

ABSAROKIUS ABBOTTI (Loomis), 1906
Figure 4, A–B

Holotype:—Amherst 3479, a fragment of the right ramus containing P_3-M_3.

Five specimens with lower teeth are referred to this species from the Amherst Lysite collections: the holotype (fig. 4A); two lower jaw fragments with P_4-M_3, Amherst 11009 and 11192; Amherst 10156, a jaw fragment containing M_{1-2}; and Amherst 11006, an isolated M_3. Although there is some variation in size, these specimens indicate a population slightly smaller than *A. noctivagus*, the Lost Cabin and La Barge species. There are minor structural differences between the two. In *A. noctivagus* (AMNH 15601) P_3 is a short oval, instead of being quadrate as in *A. abbotti*. In the later species, the molars are broad with narrow trigonids, and M_3 is longer than in *A. abbotti*, with a broad and not a narrow heel. Apparently these species are very closely related, *A. abbotti* having given rise to *A. noctivagus*.

On the whole, all the Amherst specimens are very similar to the holotype. Only very minor variation exists: in Amherst 11192 the talonid is proportionally slightly larger; in Amherst 11009 and 10156 the paraconid and metaconid are slightly more separated on M_2, apparently due to differential wear; in Amherst 10156 the external cingulum on M_2 is fairly well developed; and in Amherst 11006 the heel is broader and more like that of *A. noctivagus* than in the other specimens.

A maxillary fragment containing RM^{2-3} is associated with the holotype of *A. abbotti*. The museum number is worn off the specimen, so that it is impossible to determine whether it bears the same number as does the holotype lower jaw. Loomis does not mention this fragment in the original description of *Anaptomorphus abbotti* (1906, p. 278). No mention is made of it in the catalog of the Amherst collection. Nevertheless, it is obvious that the upper teeth were identified by Loomis as *A. abbotti* and placed with the type lower jaw fragment. Amherst 10201 is a well preserved maxillary with LP^3-M^3 collected by F. D. and H. E. Wood from the type locality of the Lysite, the last two molars of which agree perfectly with the unidentified specimen above. Furthermore no. 10201 occludes almost exactly with Amherst 11192, one of the well preserved lower jaw fragments. These upper teeth may therefore be considered to be those of *A. abbotti*. The upper teeth of this species have not previously been described.

All the upper teeth are wide transversely (fig. 4, B). P^3 and P^4 are large, the latter being larger than M^1 and with as great an area as M^2. The external portions of the premolars are long and the internal heels short. On the external half of each tooth is a large, high cusp from which a blade descends posteriorly. The protocone is much smaller and lies at the antero-internal border. From it runs a low sharp crest along the anterior border of the tooth to a faint parastyle on P^3 and a moderate one on P^4. Posteriorly, crests from the protocone run across the lingual border to end at the postero-internal corner of the tooth. There are faint traces of broken external cingula on both premolars.

M^1 and M^2 have a modified heart shape—the external borders of each tooth bulge around the paracone and metacone, while the lingual border is more pointed. The internal border of M^1 is relatively straight, whereas that of M^2 is rounded. On both teeth, the protocones are set well in from the lingual margin and are strong. The conules are forked, low, and poorly developed. The paracone and metacone are large, subequal and distinctly separated. The parastyle of M^1 is small, and the external cingulum faint. On M^2, the external cingulum is small. On both teeth there are well developed anterior and posterior cingula. At the lingual end of each posterior cingulum is a very small rise suggesting a prospective hypocone. M^3 is very small and triangular with a narrow

internal apex, no visible metaconule and very faint protoconule. There is a minute external cingulum, and well developed anterior and posterior cingula.

The teeth differ from those of *A. noctivagus* in having external cingula, in the small parastyle on M^1, the shape of the external border, the narrow internal margin of M^3, and the antero-posterior extension of the external portion of P^4.

In many respects Amherst 10201 is similar to *Tetonius homunculus* but differs in the narrower lingual portions of the molars, the small protocone of P^4, the poorly developed cingula, and the fact that in the Lysite form the hypocone is not even rudimentary. This species could be considered as intermediate between *T. homunculus* and *A. noctivagus*.

A. abbotti differs from *Paratetonius steini* (Seton, 1940, fig. C) in having a small protocone on P^3, no transverse median ridge from the primary cusp on P^4, less well developed cingula on the molars, a parastyle on M^1, and perhaps better developed conules on the molars, and finally in the shape of P^3 and P^4.

The upper teeth seem to strengthen Matthew's supposition that the series *homunculus-abbotti-noctivagus* is a genetic one; but the differences in the anterior teeth show that *Absarokius* represents a generically distinct line leading away from *Tetonius*.

Omomys minutus (Loomis) 1906
Figure 4, C

The holotype of *O. minutus* (Loomis), Amherst 3365, is still the only specimen of this form in the Amherst collections. The three specimens of *O. minutus* mentioned by Loomis in 1906 as having been found on Bridger Creek are neither listed in the Amherst Museum card catalogue nor could they be found anywhere. Loomis (1906, p. 283) originally described this species as *Notharctus*. Matthew (1915c, p. 450) referred it to *Omomys* because of the pattern of the molars, and the moderate width and absence of crowding as shown by the premolar roots.

Simpson in his discussion of the affinities of *Loveina zephyri* states (1940, p. 189): "The question arises whether the Lower Eocene species previously tentatively referred to *Omomys* (a Middle Eocene genus) do not belong rather to *Loveina*. These species are *?Omomys vespertinus* Matthew, 1915, and *?Omomys minutus* (Loomis, 1906). In neither of these are antemolar teeth known and without these the generic assignment is highly uncertain. It is unlikely that either really belongs in *Omomys*. *?Omomys minutus* is surely a different species from the other two in question. Its more elongate alveoli for P_{3-4} suggest that these teeth were unlike those of *Loveina zephyri* and make common generic assignment uncertain. Loomis' species is still *incertae sedis* and may be left questionably in *?Omomys* pending discovery of better material."

There certainly seems to be no specific and little generic similarity between *O. minutus* and *Loveina zephyri*. The roots of P_{3-4} indicate relatively long narrow teeth, differing from *L. zephyri* as mentioned by Simpson. In *O. minutus* the paraconid of M_1 is more strongly developed and separated from the metaconid, and there are strong cingula along the buccal half of the tooth.

The type specimen seems to agree with *Omomys* very well in the comparable teeth, especially in the strong, fully separated paraconids, the marginal position of many cusps, the strong external cingulum, and probably in the size of the premolars.

Family Adapidae
Genus Pelycodus Cope, 1875
Figure 4, D–E

Eight Amherst specimens from the type locality of the Lysite are referred to this genus. The species of this genus and of *Notharctus* intergrade almost continuously. Most previous authors establish the line of division between the two genera arbitrarily at the end of Lysite time (Matthew, 1915c; Granger and Gregory, 1917). Simpson (1929b, p. 9), however, records *Pelycodus* as ranging from Sand Coulee to Lost Cabin. The almost complete gradation from the earlier genus to the later one involves not only an increase in size of the teeth but a series of structural changes, including the gradual reduction of the paraconid on the lower molars and the increased development of the hypocone and mesostyle on the upper molars. The morphologic stages overlap in time: for example, the rare more ad-

vanced specimens of an earlier population reflect the normal condition found in the next later population. This of course is the perfect case of the differences between horizontal and vertical classifications.

Two species of *Pelycodus* are reported from the Lysite, *P. frugivorus* and *P. jarrovii*. Unfortunately in the Amherst collections only a few specimens can be referred to *Pelycodus*, and although they show variations, especially in the heel of M_3, nothing can be done in determining whether there are differences in frequency distributions of particular variations between the two species. The variations are said to be similar and common to both species, and so essentially there is no difference between the two except in size of the lower molars. Matthew (1915c, p. 441) in discussing *P. frugivorus* states "I can find no distinction except the smaller size and less robust proportions." Under "Key to species of *Pelycodus*" (p. 436) Matthew lists the ranges in size as:

"M_{1-3}=14–16 mm."—*P. frugivorus*
"M_{1-3}=16–18 mm."—*P. jarrovii*

Most of the material at Amherst from the typical Lysite consists of isolated lower molars. It is very difficult to determine with certainty which species they represent as they are intermediate in size between the figured referred specimens. There are, of course, various combinations of measurements of each of the three lower teeth that will give a total measurement within the range established for one or the other species. The only specimen in the collection including M_{1-3} lies just within the range for *P. jarrovii* (Amherst 3542, fig. 4, D). This is unquestionably the specimen figured by Loomis as *P. nuniensis* (1906, fig. 5).

Comparisons were made between Amherst 3542, representing *P. jarrovii*, and Amherst 3414, a jaw fragment containing P_3–M_3, which is the specimen figured by Loomis (1906, fig. 3) as *P. frugivorus* (from Gray Bull or Lysite equivalent in Buffalo Basin). The length of M_{1-3} of the latter specimen is 15.46 mm., and the specimen is considerably less robust than Amherst 3542. Six specimens were assigned to *P. jarrovii* and two to *P. frugivorus* (fig. 4, E). Very possibly there is only one species present in the Lysite, but more adequate material is needed to demonstrate this.

PRIMATE, Incertae sedis
Genus PHENACOLEMUR Matthew, 1915
PHENACOLEMUR sp.
Figure 4, F

A single specimen from the Loomis collection of 1904, Amherst 3463, is identifiable as *Phenacolemur*. In the box with the specimen was a label reading "*Phenacolemur citatus* gen. et. sp. indesc. Fam. Apatemyidae."

The specimen consists of a large portion of the right jaw with the alveoli for P_4, M_1, and M_3. The only tooth present is M_2. Original identification as *Phenacolemur* seems to be correct. The specimen is extremely small; there is no visible paraconid on the preserved tooth; the four major cusps are widely separated; and the hypoconid and entoconid are at the borders at the posterior corners of the teeth .There is no hypoconulid present although there is a very faint rise of the hypolophid just internal of the hypoconid, the posterior mental foramen is beneath M_1, and the jaw is deep and short. M_2 is proportionately considerably smaller than the corresponding tooth of *P. citatus*, but agrees well with it in structural detail. However, the Amherst specimen may represent another, smaller, species in the Lysite. Undetermined specimens of *Phenacolemur* have previously been reported from the type Lysite. The measurements of the tooth are as follows: M_2 anteroposterior 2.31 mm., transverse 1.8 mm.

Order RODENTIA
Family PARAMYIDAE

A revision of the paramyids is under way by the junior author, so only a summary will be given of the species identified from the Lysite.

Genus PARAMYS Leidy, 1871
PARAMYS MAJOR Loomis, 1907

Paramys primaevus Loomis, 1907.
Paramys quadratus Loomis, 1907.

Holotype.—Amherst 327a, lower jaw with P_4–M_3.

Referred specimens.—Amherst Nos. 3238, 10136, 10174, 11012, 11039, 11113, 11114, 11136, 11137, 11175 and 11278.

PARAMYS BICUSPIS Loomis, 1907

Holotype.—Amherst 451, lower jaw with RM_{1-3}, maxillary with LP^4–M^2.

Referred specimens.—Amherst Nos. 3181, 11011, 11076, 11090, 11104, 11135, 11195, 11279 and 11280.

PARAMYS EXCAVATUS Loomis, 1907

Holotype.—Amherst 327, lower jaw with P_4–M_3.

Referred specimens.—Amherst Nos. 3331 and 11162.

Genus LEPTOTOMUS Matthew, 1910
LEPTOTOMUS, n. sp.

Holotype.—Amherst 3334, lower jaw with RM_{2-3} and incisor, being described later.

Incertae sedis
"SCIURAVUS" DEPRESSUS Loomis, 1907

Holotype.—Amherst 432, partial skull.

Referred material.—Amherst Nos. 458, 487, 10077, 10135, 11010, 11245, 11275, 11276 and 11277.

This form is not *Sciuravus*, but its affinities are by no means clear at present.

Order CARNIVORA
Family ARCTOCYONIDAE
Genus THRYPTACODON Matthew, 1915

A single specimen, Amherst 3391, represents this primitive carnivore in the Lysite. Members of the genus until recently have been described only from the Gray Bull, although Van Houten (1945, p. 452) questionably refers a specimen from the Lysite horizon in the Big Horn Basin to this genus. Gazin (1952, p. 50) describes a specimen from the upper Knight, extending the range to the Lost Cabin level. The Amherst specimen consists of jaw fragments containing lower teeth that show the typical characteristics of the genus.

Two species have been referred to this genus, *T. antiquus* and *T. olseni*. Of these two species the lower teeth are known only from the smaller *T. antiquus*. The Amherst specimen differs only in details in the pattern of the teeth, but is considerably smaller. This size difference is sufficiently great to warrant specific separation.

THRYPTACODON LOISI Kelley & Wood, n. sp.
Figure 5, A–C

Holotype.—Amherst 3391, three jaw fragments each containing a tooth. The teeth represented are LP_4, LM_2, RM_3. If more than one individual is involved, the fragment containing LM_2 is designated as the holotype. Collected along Bridger Creek by Loomis in 1904.

Diagnosis.—Teeth nearly quadrate; P_4 with very small basal paraconid; strong wing extending inward from protoconid and swinging posterad to connect with posterior cingulum; hypoconid small; large anterior cingulum; paraconid of molars median; continuous external cingula; heel of M_2 wide with large hypoconid and entoconid; hypoconulid absent; hypoconid of M_3 only slightly smaller than trigonid cusps; entoconid smaller than hypoconid; hypoconulid moderately large.

Remarks.—This species is 10–20 percent smaller than *T. antiquus*. In addition, it differs in the internal wing of the protoconid of P_4, the metaconid being larger than the protoconid on M_2, and in the small size or absence of the hypoconulid of M_2.

	Measurements (mm.)		
	LP_4	LM_2	RM_3
Anteroposterior	4.9	5.6	5.5
Transverse	3.3	4.4	3.9

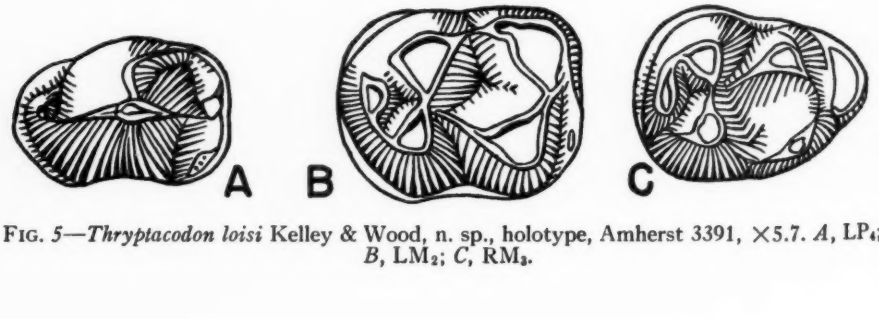

FIG. 5—*Thryptacodon loisi* Kelley & Wood, n. sp., holotype, Amherst 3391, ×5.7. *A*, LP_4; *B*, LM_2; *C*, RM_3.

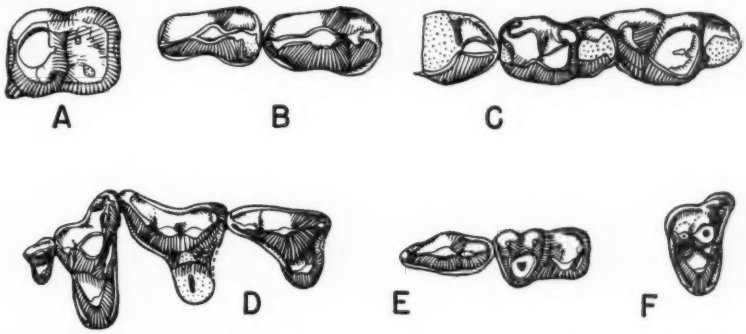

FIG. 6—Teeth of Carnivores, mostly ×1. *A*, *Anacodon ursidens*, Amherst 3382, RM_2; *B*, *Oxyaena ultima*, Amherst 3526, RP_{3-4}; *C*, *O. ultima*, Amherst 3370, LP_4–M_2; *D*, *Prolimnocyon elisabethae*, Amherst 11225, RP^4–M^3, ×2, Anterior to right; *E*, *Didymictis altidens lysitensis*, Amherst 11181, LP_4–M_1; *F*, *D. a. lysitensis*, Amherst 11120, RM^1. Anterior to right.

ANACODON URSIDENS Cope, 1882
Figure 6, A

Both species of this genus are found in the Big Horn Basin Lysite equivalent. No record has previously been made of its occurrence in the type Lysite.

Amherst 3382, an isolated second lower molar is easily identified as *Anacodon*, and is referred to this species on the basis of size. It is too small to be an M_2 of *A. cultridens* and too large to be an M_1 of that species. It is only slightly larger than the M_2 referred to *A. ursidens* by Matthew (1915a, fig. 10). The molar cusps are flattened and almost obscured, and there is a basal anterointernal projection of enamel similar to that found in the corresponding tooth of *A. ursidens*.

Family OXYAENIDAE
OXYAENA ULTIMA Denison, 1938
Figure 6, B–C

Four specimens from the Amherst collections are referred to this form. All are fragmentary and badly worn. The two most complete specimens are Amherst 3526, consisting of isolated P_3, P_4, and badly worn M_1 (fig. 6, B); and Amherst 3370, a lower jaw fragment containing the posterior portion of P_4, and worn M_{1-2} (fig. 6, C). A specimen from the Lysite equivalent of the Big Horn Basin was referred by Matthew (1915a, p. 55) to *O. pardalis*. This species was considered a synonym of *O. forcipata* by Denison (1938, p. 169). He also refers a specimen from the type Lysite to *O. lupina*, although it is a little large for that species. Measurements of Amherst 3526 and 3370 show them to be intermediate between *O. forcipata* and *O. ultima* of the Lost Cabin of the Wind River Basin.

The teeth are much too large to be considered as *O. lupina*. Denison states that *O. ultima* "is the size of *O. forcipata*, from which it differs markedly in the slender, compressed lower premolars; W/L of P_4 is only 0.52, as compared to 0.57–0.60 in *O. forcipata*. This character agrees better with *O. lupina*, of which this species may be a large derivative" (op. cit., p. 171). The present material has a W/L of P_4 of 0.57, agreeing with *O. lupina* and falling at the lower end of the range of *O. forcipata*. The basal anterior cusp of P_4 is small (fig. 6, B), agreeing with *O. forcipata* or *O. lupina*. However, Amherst 3370 agrees more closely with *O. ultima* is the proportions of the trigonid of M_2, and perhaps in the extremely small talonid of M_2 (fig. 6, C). The ratio of M_1/M_2 could be used to assign it to either species, and in size of teeth it is perhaps slightly closer to *O. ultima*. The metaconid of M_2 is vestigial and the protoconid extremely large, again allying the specimens with *O. ultima*. Finally the depth of jaw under M_2 is approximately equal to that of *O. forcipata* and is almost exactly intermediate between the depth of *O. lupina* and *O. ultima*.

From the above discussion it seems quite certain that these Lysite specimens are in-

termediate between *O. forcipata*, *O. lupina* and *O. ultima*, although somewhat closer to the last. It is possible that in the Lysite population we are dealing with an intergrading series of variations that is as a whole intermediate between *O. lupina* and *O. ultima*. Assignment is made to the latter species because of the vestigial metaconid and small talonid of M_2, and the slenderness of the teeth in general, particularly of M_2.

Family Hyaenodontidae
Prolimnocyon elisabethae Gazin, 1952
Figure 6, D

The fragments of a maxillary, Amherst 11225, with LP^4-M^3 are referred to this species. The upper teeth of this genus have been poorly known and not very satisfactorily illustrated, but there seems little doubt but that this specimen belongs to the genus. Matthew described the upper teeth as follows: "M^2 is transverse, nearly as wide as m^1, the metacone vestigial, parastyle long and curved. M^3 is represented by two alveoli which indicate a tooth one-half or one-third the transverse width of m^2. M^1 is much like the corresponding tooth in *Sinopa*, but with *me* and *pa* more closely connate. P^4 is 3-rooted triangular, smaller than m^1; . . ." (1915a, p. 69). Denison (1938, p. 178) reverses the characters of the metacone and parastyle of M^2, which seems to have been a lapsus calami, as the present material agrees with Matthew's description. In this specimen, M^2 is wider than M^1, in contrast to the situation in AMNH 15171 (Matthew, 1915a, fig. 60). External cingula are present on all the teeth, and anterior and posterior cingula on M^2. M^3 is greatly reduced, with one external and one internal root, partially fused. The tooth apparently is smaller than in the material from the Gray Bull, which would fit with this specimen being intermediate between the Gray Bull *P. atavus* and the Lost Cabin *P. antiquus*. The resemblances are very close to *P. elisabethae* from the La Barge fauna, and the Lysite material may be referred to Gazin's species. Since the La Barge fauna represents an early level of Lost Cabin time, it is not surprising that the Lysite material is closer to the La Barge *Prolimnocyon* than to that of the typical Lost Cabin.

Family Miacidae
Didymictis altidens lysitensis (Matthew), 1915
Figure 6, E–F

There seems to be no question as to the phylogenetic position of this form. It is intermediate between the Gray Bull. *D. protenus* and *D. altidens* of the Lost Cabin. The only question could be the taxonomic means of indicating this. Matthew (1915a, p. 21) achieved this by making it a subspecies of *D. protenus*. Simpson (1937, p. 15) considered that it falls more nearly within the limits of *D. altidens*, of which he made it a subspecies.

Seven specimens are referred to this species, Amherst 11181, a jaw fragment with P_4–M_3, being the most complete (fig. 6, E). In several isolated M^1s, the internal cingulum is interrupted lingually (fig. 6, F) in contrast to Matthew's type, where it is continuous. Measurements of the Amherst specimens were compared with those of the published figures. Every specimen was smaller than the holotype of *D. altidens lysitensis* from the Big Horn Lysite level; and insofar as comparisons could be made, they were closer to *D. protenus curtidens* of the Gray Bull. With the limited number of specimens available, and without figures on the range of measurements in the populations from the type localities, it is impossible to determine whether the Wind River specimens represent the small end of the distribution curve of the Big Horn subspecies, or whether there is a geographic difference in size between the populations of the two areas.

Order Condylarthra
Family Phenacodontidae
Genus Phenacodus Cope, 1873

The specimens referred to this genus are exceedingly variable, and do not present a clear taxonomic picture. Generally the teeth show numerous well developed accessory cusps, but these are usually absent in the Amherst Lysite material. Granger states (1915, p. 332–335)

> Together they present a bewildering array with their great variation in size and in the lesser characters of the teeth which in many groups would constitute good specific differences but which here often appear to be only

TABLE 1.—MEASUREMENTS (MM.) OF *Didymictis altidens lysitensis*

Amherst No.	P_3		P_4		M_1		M^1	
	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse
3495	—	—	—	—	—	—	8.85	13.4
11120	—	—	—	—	—	—	9.7	13.5
10173	11.0	5.45	—	—	13.5	8.4	—	—
11181	—	—	12.85	5.5	12.8	7.7	—	—

individual. The difficulty is increased by the fact that the group shows little or no evolution throughout its range. The last survivors in the Lost Cabin beds cannot be separated specifically from those forms of the same size in the Clark Fork, where the genus makes its first appearance. There are obviously several species, indicated by size and the relative proportions of the teeth, and in one or two cases by premolar characters of rather doubtful constancy.

Four species have been identified from the Lysite or its equivalents: *P. p. primaevus*, *P. copei*, *P. vortmani* and *P. brachypternus*. There are only 10 specimens of the genus in the Amherst collections, which include materials falling within the definition of each of these "species."

P. primaevus primaevus is clearly separable from the other species on the basis of its larger size. The other three forms do not show any sharp demarcations, intergrading in size and cusp pattern.

It is quite conceivable that these last three species in the Lysite include different sexes, or portions of a relatively continuous population centered in size about *P. vortmani*, a situation very similar to what has been found to exist in the variable *Hyopsodus* of the Lysite. It is not probable that four species of the same genus of relatively large animals would have existed simultaneously in approximately the same area. Ecological barriers could be supposed between the very large *P. primaevus primaevus* and the other "species"; but it is doubtful that they existed between *P. copei*, *P. vortmani*, and *P. brachypternus* during the Lysite. Due to the scarcity of fossils of this genus in the Amherst collection, it has not been possible to analyze it statistically. Therefore, the specimens are here referred to the species that they most nearly represent in size, with the expectation that additional material will permit a reduction of the number of species.

It was also noticed that very few of the Amherst specimens exhibited the *Phenacodus* characteristic of well developed accessory cusps.

PHENACODUS PRIMAEVUS PRIMAEVUS Cope, 1873

Figure 7, A

A fourth lower premolar, Amherst 3025, and a jaw fragment with parts of M_1 and M_2, are referred to this form on the basis of size. They are very similar to the corresponding teeth of the skeleton in the American Museum (Granger, 1915, fig. 3). These specimens apparently are the first representation of this species in the Wind River Lysite.

PHENACODUS COPEI Granger, 1915

Figure 7, B

Six specimens in the Amherst Museum from the Lysite have been referred to this species largely on the basis of size (see Table 2). Amherst 3531, a lower jaw fragment containing M_{1-3}, agrees with the holotype fairly well in all characters. Amherst 10121, a jaw fragment with P_4–M_1, has the transverse diameter of the teeth narrower than in the type, which may in part be due to the poor condition of the specimen. Amherst 11241, an isolated M_3, is between *P. vortmani* and *P. copei* in size, and would fit either species, structurally. Since it agrees well with the corresponding tooth of Amherst 3531 it is referred to *P. copei*. Amherst 11222, ?M_2, is also intermediate in size between *P. vortmani* and *P. copei*, and is arbitrarily referred to the latter species. An upper fourth premolar and second molar are referred to this species on the basis of Granger's figures.

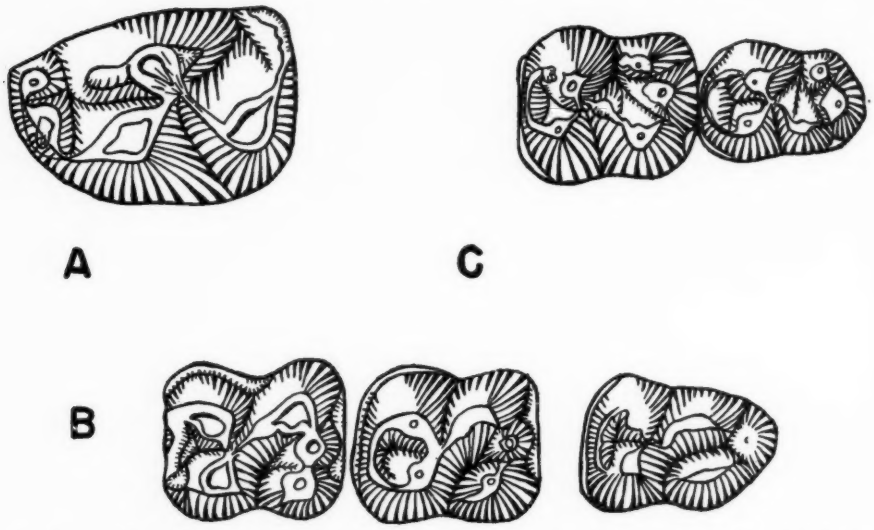

FIG. 7—*Phenacodus*, ×2¾. *A*, *P. primaevus primaevus*, Amherst 3025, LP_4; *B*, *P. copei*, Amherst 3531, RM_{1-3}; *C*, *P. vortmani*, Amherst 3326, LM_{2-3}.

PHENACODUS VORTMANI (Cope), 1880
Figure 7, C

Two specimens from the Amherst collections are tentatively referred to this species on the basis of size; one, a single lower second molar slightly larger than Granger's topotype; the second, a jaw fragment with M_{2-3}. The latter shows an interesting variation in the proportions of M_3, which is quite narrow relative to its length. It is similar in this respect to the Wind River specimen figured by Cope (1885, pl. 58, fig. 8).

PHENACODUS BRACHYPTERNUS Cope, 1882

One lower fourth premolar has been referred to this species from the Amherst collections. It differs from Granger's figure (1915, fig. 6) only in two minor variations: the paraconid is but moderately developed and it is slightly smaller in size. A jaw with a badly worn molar is tentatively referred here.

With only a single unworn specimen referable to this species, it is impossible to determine whether it represents the extreme small portion of a variable *P. vortmani* population. Nevertheless, at present this specimen may be referred to *P. brachypternus* on the basis of its extremely small size. It is considerably larger than the largest *Hyopsodus*.

Family HYOPSODONTIDAE
Genus HYOPSODUS Leidy, 1870

In the Amherst collections there are 126 specimens of this genus identifiable as to species. Isolated incisors, canines, anterior premolars, and fragmentary teeth not certainly specifically identifiable would bring this number above 250 specimens.

Five members of this genus were identified from the Lysite or equivalent beds by Matthew (1915b, p. 326) and Van Houten (1945, p. 456): *H. powellianus powellianus*, *H. p. browni*, *H. wortmani minor*, *H. mentalis mentalis* and *H. m. lysitensis*. All of these were identified by Matthew as present in the Wind River Lysite.

From the latest revision of *Hyopsodus* (Matthew, 1915b), it is evident that the relationships between the species of the genus are unknown. There is great variability both in size and in cusp pattern, with no clear trends visible.

In identifying the Amherst material, it was found that specimens could be assigned to particular species with great difficulty. The holotype of *H. minor* was quite different from everything else, and represents a separate unit. The remaining specimens represent samples of a highly variable population that were very close to each other in cusp pattern and size. Four preliminary groups

TABLE 2.—MEASUREMENTS OF LOWER TEETH OF *Phenacodus* IN MM.

Specimen	P_4		M_1		M_2		M_3	
	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse
P. primaevus AMNH 4369	13.7	9.0	13.3	10.65	13.7	12.0	13.7	10.7
P. p. primaevus Amherst 3025	13.5	9.5	—	—	—	—	—	—
P. copei AMNH 4378	8.8	8.8	8.75	6.9	9.5	7.5	9.7	6.7
P. copei Amherst 3531	—	—	8.85	7.6	9.15	7.6	9.5	6.6
P. copei Amherst 10121	9.2	7.0	8.8	6.0	—	—	—	—
P. copei Amherst 11241	—	—	—	—	—	—	9.15	6.85
P. cf. *P. copei* Amherst 11222	—	—	—	—	8.8	7.95	—	—
P. vortmani . Amherst 11045	—	—	—	—	8.5	7.5	—	—
P. vortmani Amherst 3326	—	—	—	—	8.4	7.5	8.45	6.0
P. vortmani AMNH 2983	8.0	5.5	—	—	8.0	7.0	9.0	6.5
P. brachypternus AMNH 15315	7.2	4.4	6.8	5.45	6.2	5.3	6.2	4.1
P. brachypternus Amherst 10200	6.9	3.8	—	—	—	—	—	—

were separated on the basis of the antero-posterior diameter of the teeth and overall cusp pattern, in an attempt to identify the forms previously reported from the Lysite. Although the variability of the characters involved in the cusp pattern enable many of the specimens from each group to be similar to more than one holotype, in general the specimens from one group were similar in cusp pattern to the holotype to which they were assigned on the basis of the antero-posterior diameter grouping. The smallest of these groups was *H. wortmani wortmani* which included many of the specimens identified as members of this species by Loomis in 1905. The next larger group was considered as being *H. mentalis lysitensis*, the next to largest as being *H. powellianus browni*, and finally the largest of the populations as *H. powellianus powellianus* (including *H. jacksoni*, the cotypes of which are not separable from this species).

Statistical analyses were made to determine whether these four populations could be considered natural.[1] Graphs were made for each tooth with antero-posterior diameter plotted against transverse diameter. The two smallest groups and the two largest groups overlapped considerably, the only clear cut separation being in the middle of the series. Regression lines, on the basis of the two measurements, were determined, but showed no more than an expected proportional increase between antero-posterior and transverse diameters similar in all populations.

Population curves were then made using both 0.2 mm. and 0.5 mm. differences in tooth length, for each tooth. Both sets of graphs showed a similar situation, i.e. that the population was generally divisible into two groups. This was most apparent in the lower teeth, at least partially due to the larger sample available (fig. 8). For P_3 and

[1] Only certain of the statistical analyses and their results are included in this paper. A complete account of the statistical treatment of *Hyopsodus* and *Hyracotherium*, including the method of setting up the data and detailed discussion of the results, is on file in the Amherst College Library in a thesis entitled "Population Studies on Horses and Hyopsodonts of the Lower Eocene Lysite Fauna," by the senior author. Probability values of less than 0.05 were taken to indicate significant differences.

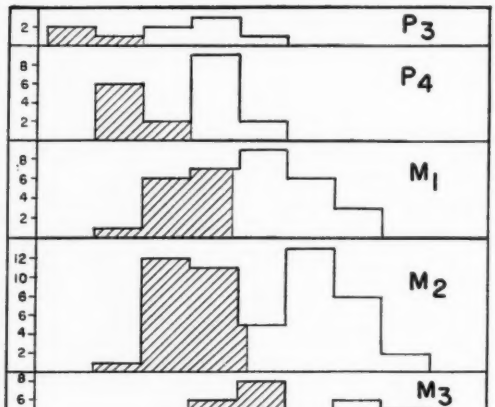

FIG. 8—Size variation of lower teeth of Lysite hyopsodonts. Shaded areas *Hyopsodus mentalis*. Ordinate = number of specimens, abscissa = tooth length in mm.

M_1, which show no breaks in the curve with 0.5 mm. interval, there are clear breaks on the curves using the smaller interval. Means and deviations were computed, but did not produce useful data in determining the number of forms present.

For facility in discussion, the four tentative populations mentioned above are referred to as populations "a," "b," "c," and "d"; population "a" representing the smallest forms tentatively identified as *H. wortmani wortmani;* population "b," the next larger; and so on. Also the combination of "a" and "b" will be referred to as population 1 and the combination of "c" and "d" will be referred to as population 2.

Observation of the 0.2 mm. population curves for both upper and lower teeth showed that population "a" was separated from "b" by a 0.2 mm. class in only one out of ten curves, "b" from "c" in eight out of ten curves, and "c" from "d" in three out of ten curves. A Chi Square test was run on these data to determine whether this distribution of separations between consecutive populations could be obtained through random collection. The result of this test showed that the low amount of separation between "a" and "b" or between "c" and "d" is not statistically significant; but that the separation within populations 1 and 2 is significantly different from the separation between them. This indicates that there are two variable populations and not four.

There is considerable variation between the four groups in the position of the greatest transverse diameter of M_1 and M_2, it being sometimes across the trigonid, and at others across the talonid. Chi Square analysis showed that the distribution of the variation in widest point of the tooth is significantly not a factor of random sampling, and that, in particular, population "a" was significantly different from the other three in having the greatest transverse diameter across the talonid in almost all specimens.

The most noticeable variations, however, were those of the cusp pattern, which is very variable. An extreme example is the variation from no metaconid to a fairly well developed metaconid on P_4 of population "a." In general there was variation in the following characters:

A. Lower teeth
   1. Presence of a paraconid (from P_3 to M_3 inclusive)
   2. Condition of the metaconid on P_4
   3. Hypoconid size and complexity on P_3 and P_4
   4. Entoconid presence and condition exclusive of P_3
   5. Cingulum development
   6. Condition of the heel of M_3 (whether stout or narrow)

B. Upper teeth
   1. Shape of P^3 and P^4
   2. Parastyle development of P^3 and P^4
   3. Development of hypocone on molars
   4. Cingulum development
   5. Shape of M^3

C. In general
   1. Height and separation of cusps
   2. Strength of lophs

Many of these variable characters could not be treated statistically because of inability to divide them into measurable units; the slight amount of variability with little or no specific pattern; the presence of variability which could be accounted for by wear; or combinations of these.

Five of these 13 characters, all involving lower teeth, were treated statistically in the hope that a certain limited range of variability could be assigned to a population that

would distinguish it from the others. It is important to emphasize the tremendous variability in these characters. The five characters studied were: size and independence of metaconid of P_4; condition of hypoconid of P_4; development of entoconid of P_4; development and independence of entoconid of M_3; and presence of a paraconid on P_4–M_3 inclusive.

This analysis showed that the development and separation of the metaconid of P_4, the development of the entoconid of M_3, and the presence of paraconids are equally variable in all of the four tentative populations. Population "b" tends to have a more highly developed hypoconid on P_4 than do the other three. Population 1 is distinguished from population 2 by having a more highly developed entoconid on P_4. There seems to be a progressive gradation from a well developed entoconid in population "a" to a less well developed cusp in population "d," with populations "b" and "c" being intermediate. Finally, population 1 is significantly different from 2 in the more widely separated entoconid and hypoconulid on M_3.

In summary, population "a" can be separated from population "b" on the basis of the position of the maximum transverse diameter of M_1 and M_2 and of the significantly different development of the hypoconid of P_4. Although this suggests a diversification, these two characters do not appear to warrant taxonomic separation of groups "a" and "b." No statistically significant differences were found between groups "c" and "d." Samples 1 and 2 must each then be considered as single populations. Populations 1 and 2, however, can be separated on the basis of the breaks in the graphs of length by width, and in the curves of antero-posterior diameter (fig. 8). Further evidence for this separation is suggested by differences in development of the entoconid of P_4 and amount of separation of the entoconid of M_3. In no case does an associated specimen have one tooth whose measurement places it in population 1, and another tooth in population 2, although such specimens may have one tooth within group "a" or "c" while other teeth may fall within "b" or "d." The few specimens for which the length of M_{1-3} is measurable fall in two groups, a smaller population that characterizes population 1 and a larger group that characterizes population 2.

It seems justified, therefore, to assume that there are two variable species represented in the above discussion, which are here referred to *H. mentalis* and *H. powellianus*. No specimens other than the holotype could be considered as being similar in size to *H. minor*.

HYOPSODUS MENTALIS Cope, 1875
Figure 9, A–E

Certain specimens have been figured to show samples of the variations. Figures 9, A–D show gradual increase in size of the teeth. While P_4 of Amherst 11078 (fig. 9, A) has little or no metaconid, that of 11115 (fig. 9, C) shows a large and distinctly separated one, and that of 3249 (fig. 9, B) shows a very distinct metaconid. Similarly, this last has a much more prominent hypoconid and posterior cingulum than do the other specimens figured. These figures also illustrate the variability of the paraconid of both premolars and molars. Sometimes it is clearly distinct from the metaconid of the molars (fig. 9, C), whereas at other times it is very close.

The pattern of the upper molars is shown by Figure 9, E. This has somewhat less continuity in the cingula than is seen in *H. powellianus*, and is smaller. As in the lower teeth, a wide variety of variants were noted, which seemed to be of no taxonomic significance.

In the Lysite there then seems to be no reason for separating *H. mentalis* from *H. wortmani*. There is a single population, some members of which are clearly similar to the type of *H. mentalis* and others to the type of *H. wortmani*. It is beyond the scope of the present study to determine whether or not these two forms are separable in the Lost Cabin. If they should prove to be distinct, this will be a very good example of speciation in a limited period and in a limited geographic range, *H. mentalis* of the Lysite having become segregated into two populations by the Lost Cabin, which would be sufficiently distinct to be treated as separate entities.

A problem that awaits further study is to determine whether *H. mentalis* of the Lost

FIG. 9—*Hyopsodus*, ×3.27. *A*, *H. mentalis*, Amherst 11078, RP_3–M_3; *B*, *H. mentalis*, Amherst 3249, RP_3–M_3; *C*, *H. mentalis*, Amherst 11115, RP_3–M_3; *D*, *H. mentalis*, Amherst 10166, LM_{1-3}; *E*, *H. mentalis*, Amherst 3256, RP^4–M^3, anterior to right; *F*, *H. powellianus*, Amherst 3348, LP_3–M_1; P_3 figured by Loomis as *H. jacksoni*; *G*, *H. powellianus*, Amherst 3232, LP_4–M_3, holotype of *H. browni*; *H*, *H. powellianus*, Amherst 3246, RP_4–M_3, holotype of *H. jacksoni*; *I*, *H. powellianus*, Amherst 11024, RM_3; *J*, *H. powellianus*, Amherst 3232, LP^2–M^3, holotype of *H. browni*; *K*, *H. powellianus*, Amherst 3470, LM^{1-3}, "cotype" of *H. jacksoni*; *L*, *H. minor*, holotype, Amherst 3492, RM_{1-3}.

Cabin is distinguishable from the Lysite population. If it should prove to be distinct, this might be treated as a case of subspecific succession in time.

HYOPSODUS POWELLIANUS Cope, 1885
Figure 9, F–K

Hyopsodus jacksoni LOOMIS, 1905.
Hyopsodus browni LOOMIS, 1905.
Hyopsodus powellianus browni (Loomis), MATTHEW, 1915b.

In 1905 Loomis established the two species *H. browni* and *H. jacksoni* with no discussion of their relationships to *H. powellianus* other than the comparison of the three in his chart (1905, p. 424). The differences he listed are valid distinctions between the specimens, but the present study of the Lysite material shows that these are very variable characters. As indicated above, there is no reason to separate the largest forms (*H. jacksoni* or *H. powellianus*, population "d") from the next smaller group (*H. browni*, population "c").

In P_4 there is the same variability seen in *H. mentalis* (figs. 9, F–H). There is, however, always a metaconid, with greater or lesser separation from the protoconid. This cusp does not seem to be as small proportionately as Loomis thought (fig. 9G, cf. Loomis 1905, p. 422). The development of the hypoconid and entoconid is fairly uniform.

The tooth that Loomis identified as P_3 of *H. jacksoni* (op. cit., fig. 8), which Matthew considered to be "a fourth premolar of a smaller individual" (1915b, p. 322), is unquestionably a third premolar, since it is in a jaw fragment with P_4 and M_1 (fig. 9, F). It falls in the "*H. browni*" section of the size distribution.

The first two lower molars show variation in amount of fusion of paraconid and metaconid. (This is interpreted here as fusion. Perhaps it is secondary splitting of the metaconid to form a pseudoparaconid. The Lysite material looks a little more like the first interpretation, but is not conclusive.) There is not, however, any distinction of this sort that is correlated with size. Nor does there appear to be any great difference in the size of the entoconid and hypoconulid, after allowing for wear (figs. 9, F–H). There is no external cingulum on any of the lower molars.

The last molar shows great variability in the details of the posterior end. The hypoconulid may or may not unite with the entoconid, and may do it in any of several ways (figs. 9, G–I).

The upper molars (figs. 9, J–K) again show variation in size and variation in detail of the pattern, but no significant correlation between the two.

There are some suggestions of geographic differences between the hyopsodonts of the Big Horn and Wind River Basins. *H. powellianus* is from the former. Matthew states, "While the topotype series shows some variability in the form of M^3 and a few other characters they run fairly constant in size and in most characteristics" (1915b, p. 322). If this is correct, then the Amherst Lysite collection would seem to be a smaller variety, and perhaps is deserving of subspecific separation. This would not be justified without reviewing the whole problem of the hyopsodonts. Apparently the Knight specimens agree with those from the Wind River Lysite (Gazin, 1952, p. 61).

Matthew considered *H. powellianus browni* to be intermediate between *H. powellianus* and *H. mentalis*. As has been indicated above, there are other specimens from the Lysite that are much closer to *H. mentalis*. These two groups are very similar, and are undoubtedly closely related, there being very few differences other than in size. They probably diverged from a common ancestor very close to the beginning of Wind River time. Further study may lead to the conclusion that the Lysite forms are not more than subspecies, but since there are reasonably clear separations between the two, they may be considered distinct species for the present.

Loomis (1905, p. 421) mentions two specimens of this species "from the basal beds of the Wasatch of the Gray Bull River, Wyoming." No trace of these was found in the Amherst collections. Matthew (1915b, p. 322) states that "A few doubtful specimens are found in the Lost Cabin horizon." For the present, however, it seems best to conclude that this species is restricted to the Lysite and equivalent deposits.

HYOPSODUS MINOR Loomis, 1905
Figure 9, L

Hyopsodus wortmani minor, MATTHEW, 1915.

Holotype.—Amherst 3492, a fragment of a right ramus containing M_{1-3}.

Diagnosis.—Size small; molars relatively stout; anterior cingula well developed; no external cingula; protoconid and metaconid close together; cusps larger, restricting the internal basin.

Remarks.—The main characteristic of this type is the extremely small size. In no case do any other Amherst specimens approach this size. This is only partially indicated by the population curves (fig. 8). Since there is no overlap in size with *H. mentalis*, this species can be established on the basis of its extremely small size, although many of the structural characters are present in the smaller varieties of *H. mentalis* (population "a") and even in *H. powellianus*.

Since there is only a single specimen of this size category, we obviously know nothing of its range of variability. As long as there is no size overlap with *H. mentalis*, this is as distinct from *H. mentalis* as the latter is from *H. powellianus*. For the present, therefore, it must be considered to be the lone representative of a third species.

Order DINOCERATA
Family UINTATHERIIDAE
Genus PROBATHYOPSIS Simpson, 1929

Two specimens of this genus have been identified from the Lysite collection at Amherst. This is the first occurrence of the Dinocerata in the Lysite and affords a link in time between *Probathyopsis* of the upper Paleocene and lower Gray Bull and *Bathyopsis* of Lost Cabin age.

PROBATHYOPSIS LYSITENSIS Kelley & Wood, n. sp.
Figure 10, A–B

Holotype.—Amherst 11167; isolated left P_4, M_1, M_3, and talonid of M_2 and external fragment of right M_1.

Referred specimen.—Amherst 3870, jaws with LM_1 and fragments of RP_4 and RM_1.

Horizon and locality.—Holotype collected by D. R. Kelley at type locality of Lysite member of Wind River formation, July 28, 1951.

Diagnosis.—Protolophids small; no remnant of paraconid; on P_4 no swelling of external border of tooth about protoconid; hypoconulid of M_3 asymmetrically externally placed, the posterior transverse crest of moderate height and fairly continuous, heel stout with a flatly rounded posterior border.

Remarks.—P_4 is approximately the size of the corresponding tooth of *P. praecursor*, and smaller than that of *P. newbilli*. The external border of the tooth is continuous, there being no swelling around the protoconid as seen in *P. newbilli* and *P. praecursor*. The top of the worn surface of the metaconid overhangs slightly the external portion of the base of this cusp. The talonid is very similar to that of *P. newbilli*, there being a moderately developed hypoconid and a posterior cingulum that runs transversely across the posterior edge of the tooth. This last is broken into minute cusplets, the lingual one being slightly larger than the rest and representing, perhaps, the beginnings of an entoconid (fig. 10, A).

M_1 is larger than that of *P. newbilli*. The protolophid is very small. The metalophid is more transverse than in *P. newbilli* approaching the condition in *Bathyopsis*. The metaconid-metastylid complex cannot be determined due to wear and breakage. There is an elevated posterior cingulum, the lingual end of which is slightly enlarged, suggesting a faint entoconid.

The referred specimen is smaller, and may represent a different form, but seems more probably to be merely the small end of the size range. There is a short protolophid, ending in a minute cuspule (fig. 10, B). The metaconid and metastylid are distinct cusps, though close together, and soon unite with wear. There is a continuous crest from the metastylid to the hypoconid, and an almost continuous one from the hypoconid to the posterior cingulum. This tooth is much smaller than in *Bathyopsis*, and proportionately narrower. The protolophid is larger than in *Bathyopsis*. Both because of the lack of wear of this tooth and because of the very small vertical depth of the jaw, this is obviously a young individual. While it is perhaps possible that this is a milk tooth, it more probably is a small specimen of M_1.

Only a broken and badly worn talonid represents M_2. The posterior ridge extends farther linguad than in other species of *Probathyopsis*, and shows the worn outline of an entoconid. It is similar to the corresponding tooth of *P. newbilli*.

TABLE 3.—MEASUREMENTS OF TEETH IN MM.

	P_4		M_1		M_3	
	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse	Antero-posterior	Trans-verse
Amherst 11167	13.5	9.6	14.1	est. 10.3	23.0	est. 14.4
Amherst 3870	—	—	12.0	7.4	—	—

M_3 is larger than that of *P. praecursor* and smaller than in *Bathyopsoides harrisorum*. The protolophid is very small. Although the metaconid-metastylid complex is broken off, the sharp lingual rise of the wear surface of the protoconid indicates that these cusps were relatively high and suggests a condition somewhat similar to that in *Bathyopsis fissidens*. However, the cusps are the dominant feature and the lophs are secondary as is characteristic of the genus *Probathyopsis*. The posterior crest of the talonid is less continuous than in *Bathyopsis fissidens*, but more so than in *P. praecursor* (Simpson, 1929a, fig. 2). This tooth resembles *Bathyopsis* in the less rounded outline of the posterior portion of the heel, and the more externally placed hypoconulid. The crest is relatively smooth and similar to *P. successor* where "The posterior part of the heel of M_3 is wider, more rounded, and smoother than it is in *P. praecursor*" (Jepsen, 1930, p. 129).

Although this species is referable to *Probathyopsis*, it is more advanced than any other described species, especially in the reduction of the protolophid and the character of the heel of M_3, in which it is approaching *Bathyopsis*. It is possible that this species or one similar to it led to the genus *Bathyopsis* at the beginning of Lost Cabin time.

Order PANTODONTA
Family CORYPHODONTIDAE
Genus CORYPHODON Owen, 1845
Figure 10, C–D

Pieces of bone and teeth of this genus are quite abundant, most of it too badly broken to warrant collecting. The Amherst collections contain twenty-three specimens of *Coryphodon*, consisting of a few whole incisors, a few broken canines, one anterior lower premolar, and the rest associated fragments of teeth and bone.

To date, no species of *Coryphodon* has

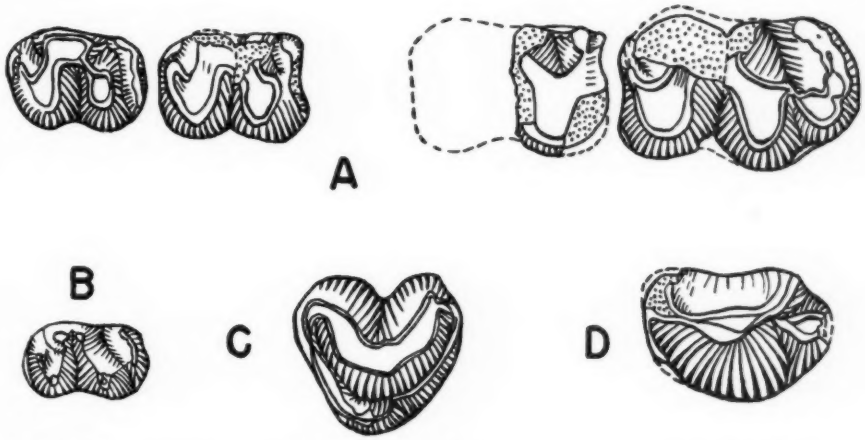

FIG. 10—*Probathyopsis* and *Coryphodon*, all ×1.4. *A*, *Probathyopsis lysitensis* Kelley & Wood, n. sp., holotype, Amherst 11167, LP_4–M_3; *B*, *P.* cf. *P. lysitensis*, Amherst 3870, LM_1; *C*, *Coryphodon* sp., Amherst 11268, RP^1, anterior to right; *D*, *Coryphodon* sp., Amherst 3378, LP_1.

been identified from the Wind River Lysite, and no species with certainty from the Big Horn Lysite equivalent (Van Houten, 1945, p. 456), although four species have been described from the Lysite equivalent of the Knight (Gazin, 1952, p. 63–64). The considerable intraspecific variability together with sexual dimorphism (Osborn, 1898; Earle, 1892) indicate the uncertainty of specific identification without much better material than is now available.

An isolated P^1 (Amherst 11268, fig. 10, C) agrees well in size and characteristics with the corresponding tooth of male *C. testis* (Osborn, 1898, fig. 22). Amherst 3378, an isolated P_1, is stout, with a relatively wide incipient talonid. There is a faint antero-external cingulum (fig. 10, D). A large upper canine, Amherst 3505, resembles that of the male *C. ventorum* in cross section.

Order PERISSODACTYLA
Family EQUIDAE
Genus HYRACOTHERIUM Owen, 1840

There are 120 specimens of *Hyracotherium* specifically identifiable from the Lysite in the Amherst Museum. Together with broken teeth, isolated incisors, canines, and anterior premolars, the population of Lysite horses represented in the Amherst collections is about 150 individuals. As is characteristic of all the Lysite collections, the material is fragmentary, consisting for the most part of single teeth with occasional fragments containing two or more teeth.

The situation is the same as with the *Hyopsodus* material. There is great variability both in size and in tooth pattern. There appear, however, to be two size groups, a smaller and more abundant one, and a large and relatively rare form. As in *Hyopsodus*, the differences show up most clearly in the lower teeth, but here the curves with 0.2 mm. interval show the gaps most clearly (fig. 11). As in *Hyopsodus*, the tooth patterns do not show consistent differences that would enable the variants to be associated with the types of described species. A statistical analysis similar to that for *Hyopsodus* was therefore undertaken.

The length of the teeth is considered more significant for the over-all evolution of the group than the width, since an increase in length of each tooth of a form would make

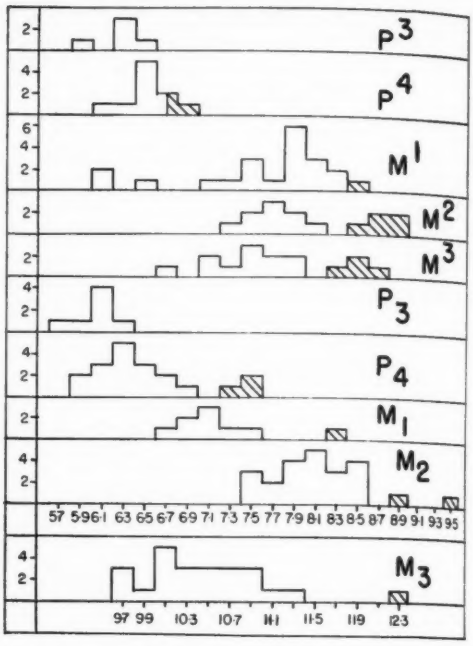

FIG. 11—Size variation of lower teeth of Lysite horses. Shaded areas *Hyracotherium craspedotum*. Ordinate = number of specimens, abscissa = length of tooth in mm.

an accumulated increase in length of the tooth row and jaw, and therefore would be related to length of the skull and over-all size increase. Examination of the curves reveals that in six out of ten curves there were two groups with no overlapping between them. The absence of a break in the other four curves may indicate overlapping in the measurements of these teeth (P^3, P^4, M^1, and P_3) or may indicate that the collections contain no specimens of these teeth from the larger form. The total jaw length of the larger form would appear to average about one and a half times that of the smaller.

Van Houten lists *H. cristatum*, *H. boreale*, *H. craspedotum* and *H.* sp. from the Lysite or its Big Horn equivalent. Gazin (1952, p. 65–67) identified *H. index*, *H. vasacciense*, *H.* cf. *venticolum* and *H.* cf. *cristatum* from the Lysite horizon of the Knight. He considers the rejection of the name *H. vasacciense* by Granger (1908) as unjustified. This seems reasonable, and Kitts (personal communication) informs us that he is following Gazin in this respect in his revision of

Hyracotherium. The common Lysite horse is very close to, if not identical with, the Knight material referred by Gazin to *H. vasacciense*, both in mean size and in range of variation (cf. fig. 11 and Gazin, 1952, p. 65), and should, according to Kitts, be referred to *H. vasacciense vasacciense*. One of the few differences between the faunas of the Knight and the type Lysite is the presence of *H. index* in the former. No specimens that could conceivably fall within the range of size of this species are present in the Amherst collections.

Not a single tooth in the Amherst collection is anywhere near as large as the corresponding tooth of the holotype of either *H. cristatum* or *H. craspedotum*. The smaller and more abundant form agrees in size with *H. boreale*, and the holotype of that species falls within the range of variability represented by the Amherst Lysite material. The population of larger individuals is closer in antero-posterior diameter to the Lost Cabin *H. vasacciense venticolum* than to the New Mexican *H. cristonense*. However, the cusp pattern of the teeth of the larger Lysite forms is close to that characteristic of *H. cristonense*. Kitts informs us that this material seems identical to the larger Lost Cabin horse, which should be called *H. craspedotum*, and that name is therefore used for the larger Lysite horse, even though it is considerably smaller than the type of the Lost Cabin species.

Hyracotherium vasacciense (Cope), 1872
Figure 12, A–I

From the Amherst collections 96 specimens are referred to *H. vasacciense*. Although there is general similarity, no two teeth are identical in size or cusp pattern. Apparently, as Granger has already indicated (1908, p. 242–244), we are dealing here with random samples from a highly variable population.

In size, there is a maximum range of 1.7 mm., or 15 percent, in the antero-posterior diameter and of 1.6 mm., or 17 percent, in the transverse diameter of upper teeth referred to *H. vasacciense*. The bimodality or polymodality of the curves for *H. vasacciense* (fig. 11) indicates that either the limited number of specimens does not represent the full curve, or, if the sampling was at random, which it probably was, the population is undergoing radiation and speciation. The latter hypothesis seems the more likely in that some of the specimens referred to *H. vasacciense* are very similar to the later *H. venticolum* in cusp pattern although not in size.

There are variations in cingulum extent and development, height and strength of cusps and lophs, and shifting in relative position of lophs, which seem to be merely individual variants. In addition, there are the variations due to amount or distribution of wear. However, variation that seems to be significant can be seen in the heel of M_3 and the development of an entoconid of P_4.

The entoconid of P_4 ranges from being barely indicated to well developed and well separated from the hypoconid (fig. 12, A–E). Attempts were made to characterize the population on the basis of the frequency with which these variations of the entoconid occur. It would seem probable that the population of *H. vasacciense* had an approximately equal frequency of the various types of variations. A diagnostic character of the population of *H. vasacciense* would then be that the entoconid ranges from poorly to well developed.

Not only is there variation in the breadth of the heel on M_3 in *H. vasacciense* (fig. 12, D–F), but the hypoconulid varies from being single to transversely split. A Chi Square test was run to determine whether the observed frequency of variations could be obtained by random selection from a population in which the variations were equally distributed. It was seen, however, that this was not so, i.e., that the population could not be characterized by having equal distribution of the variations. We may, therefore, characterize the Lysite *H. vasacciense* as having a single hypoconulid on M_3 twice as often as any variant therefrom. The holotype of *H. boreale* (considered by Kitts to be a synonym of *H. vasacciense*) has two subsidiary cusplets split off from the hypoconulid. The Lysite specimens therefore are appreciably different from this holotype, since in only one case out of twenty-one was there a triple hypoconulid (fig. 12, F). Since no comparable population

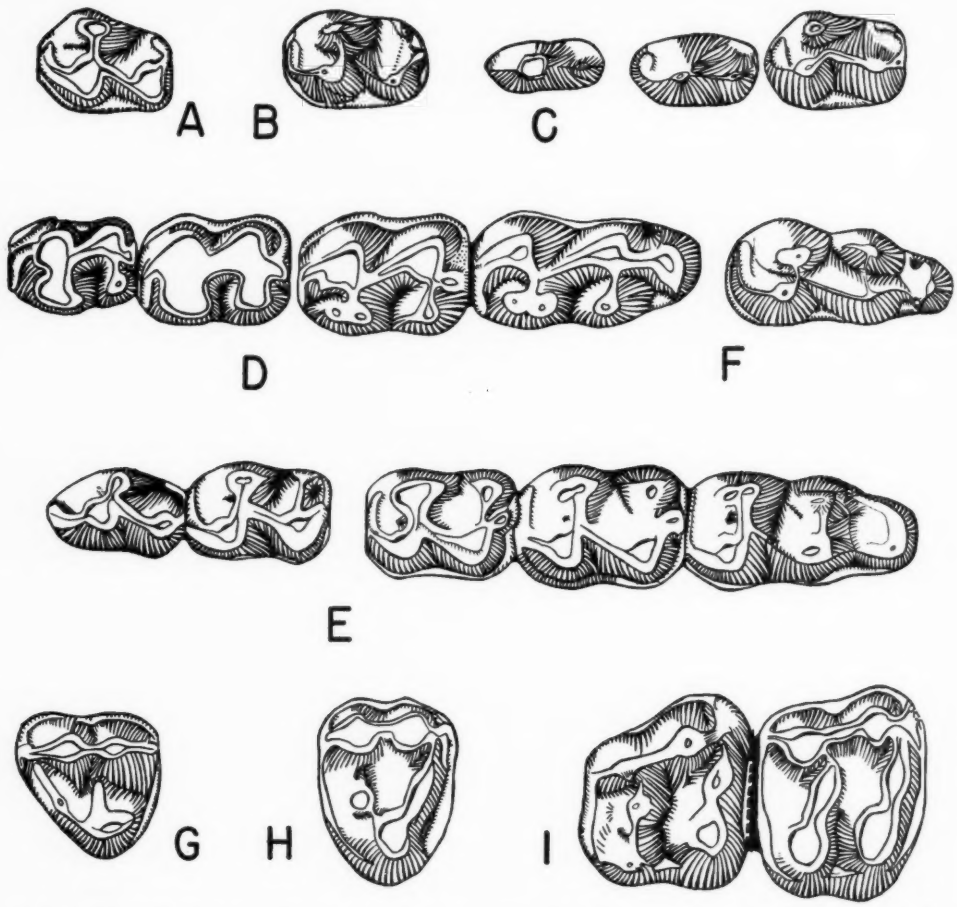

FIG. *12—Hyracotherium vasacciense*, ×3. *A*, Amherst 11085, LP_4; *B*, Amherst 10140, LP_4; *C*, Amherst 11255, LP_3–M_1; *D*. Amherst 11207, RP_4–M_3; *E*, Amherst 11179, LP_3–M_3; *F*, Amherst 10199, LM_3; *G*, Amherst 11129, RP^3, anterior to right; *H*, Amherst 11243, RP^4, anterior to right; *I*, Amherst 11243, RM^{2-3}, anterior to right.

studies have been made, it cannot be determined whether the type of *H. boreale* represents an extreme in this character, whether the Gray Bull population of *H. vasacciense* is characterized by the triple hypoconulid, or what the frequency of any of the variations may be within the Big Horn Lysite population. The single hypoconulid is found in the holotypes of *H. index* and *H. venticolum*. This may suggest a relationship of *H. vasacciense* to these two forms. It is quite possible that *H. vasacciense* is ancestral to the larger and typical Lost Cabin species, *H. venticolum*, and that the smaller and typically Gray Bull form, *H. index*, is closely related, and perhaps only subspecifically separable. The similarities between these forms were pointed out by Wortman (1896). The evolutionary relationships are beyond the limits of the present study.

In the anterior lower molars, there appear to be variations in whether or not the metaconid is doubled (fig. 12, D–E). In large part, this is due to wear, the cusp actually being crowned by two small cuspules.

The upper teeth of *H. vasacciense* are also variable in pattern, but with no significant variants. There are differences in the

strength of the parastyle and of other cusps and in the extent and development of cingula, but these appear to be partly due to insignificant individual variation, and partly to differences due to wear.

P^3 is triangular, with its apex at the lingual margin (fig. 12, G). The cingula are weak. P^4 is narrow antero-posteriorly. The lophs of the molars are very well developed, in contrast with the more cuspate condition of the larger form. In particular, the metaconule is large and forms a clear swelling on the metaloph (fig. 12, I).

HYRACOTHERIUM CRASPEDOTUM
(Cope), 1880
Figure 13, A–H

Twenty-four specimens have been tentatively referred to this species. The lower teeth are easily separable from those of *H. vasacciense* by size (fig. 11). In the upper teeth there seems to be less of a break between the two. The teeth are as large as those of *H. venticolum*, and appreciably larger than the holotype of *H. cristonense*, but differ from the former and agree with the latter in tooth pattern. They are referred to *H. craspedotum* on the authority of Kitts.

All the lower teeth of this form have a wide protolophid, and a broad anterior cingulum that reaches to the lingual border of the teeth, where it ends in conjunction with the protolophid. These features are in agreement with the type of *H. cristonense* (Wortman, 1896, figs. 11–12), whereas in *H. vasacciense* the cingulum is much narrower and generally shorter as well. Some-

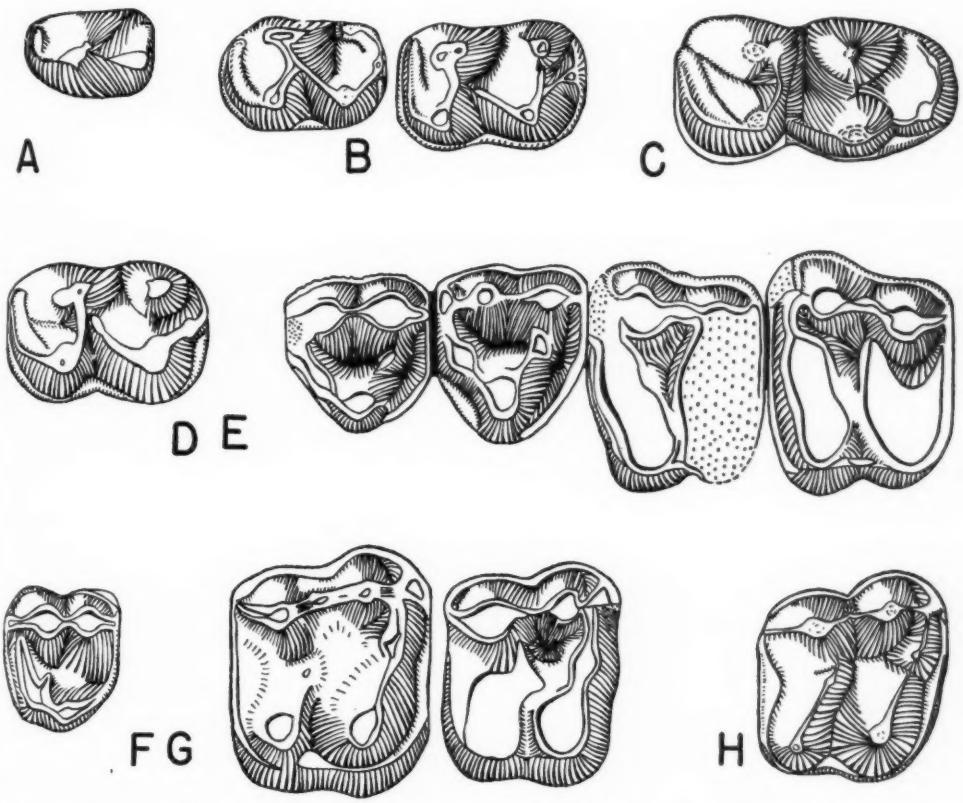

FIG. *13—Hyracotherium craspedotum*, ×3. *A*, Amherst 11160, LP_3; *B*, Amherst 10139, LP_4–M_1; *C*, Amherst 10139, LM_3; *D*, Amherst 10141, LM_2; *E*, Amherst 11046, LP^3–M^2; *F*, Amherst 11130, RP^3, anterior to right; *G*, Amherst 3349, RM^{1-2}, anterior to right; *H*, Amherst 11155, RM^3, anterior to right.

times, however, the size of the cingulum can be greatly reduced by interdental wear, so that this feature must be used with caution.

The rudimentary paraconid and large protolophid of P_3 agree with those of *H. cristonense* (fig. 13, A). P_4 has an entoconid of variable size and of variable separation as a distinct cusp (fig. 13, B). There is not, however, as much diversity as in the material referred to *H. vasacciense*, at least in part due to the smaller number of individuals available. The anterior two molars show the strong anterior cingula and wide protolophids of this form. There is variation from tooth to tooth and from specimen to specimen in the amount of connection between the hypoconid and entoconid, and in the relationships of both to the hypoconulid (fig. 13, B–D). M_3 has a broad heel bearing a hypoconulid and a lingual cusplet as in the holotype of *H. cristonense*.

Since about half of the specimens of horses from the Lysite are upper teeth, there should be some referable to *H. craspedotum*. The largest ones agree in size with those of *H. venticolum* and in pattern with *H. cristonense*, as do the lowers. There is not, however as clear a break in the size distribution as is seen in the lower teeth, although there is a separation for M^2 and M^3.

P^3 is generally rather similar to that in *H. vasacciense* except for the larger cingula (fig. 13, E). In one specimen, however, the protocone seems to have shifted posteriorly, lying behind the protoconule, as in *H. venticolum* (fig. 13, F). This condition is not as advanced as it is in the Lost Cabin form.

The upper molars show small conules, particularly the metaconules, which appear merely as slight swellings, in the lophs. The cusps in general are low and well separated, appear to be farther out on the margins of the crown than in *H. vasacciense* (figs. 13, E, G, H).

In conclusion, there are diagnostic characters in the lower teeth that enable the tentative establishment of the species *H. craspedotum* in the Lysite. The upper teeth are not diagnostic, and separation is difficult from the referred *H. vasacciense* population. The variation noted in the size of the lower teeth, and the overlapping of the two populations both in cusp pattern and size suggests the development of the Lysite *H. craspedotum* from the large variable population of *H. vasacciense*. The Lost Cabin specimens of *H. craspedotum* are considerably larger than any of the Amherst Lysite material, but are relatively close in cusp pattern to the material here referred to that species. There was then, apparently, evolution in place with increase in size.

Family Helaletidae

Heptodon ventorum (Cope), 1880

Figure 14, A–E

Fourteen specimens from the Lysite in the Amherst museum are referred to *Heptodon*, although only six are of any importance, two being portions of jaws, and four being complete crowns of premolars and molars, generally unworn. The other eight specimens are fragments of teeth.

The relationships of *H. posticus* from the Big Horn Basin and *H. ventorum* from the Wind River are not clear. There is enough variation in the few specimens at Amherst to suggest that *H. posticus* and *H. ventorum* may have been distinct in the Lysite. This is especially noticeable in the isolated upper molars. Amherst 11211, an M^2, and

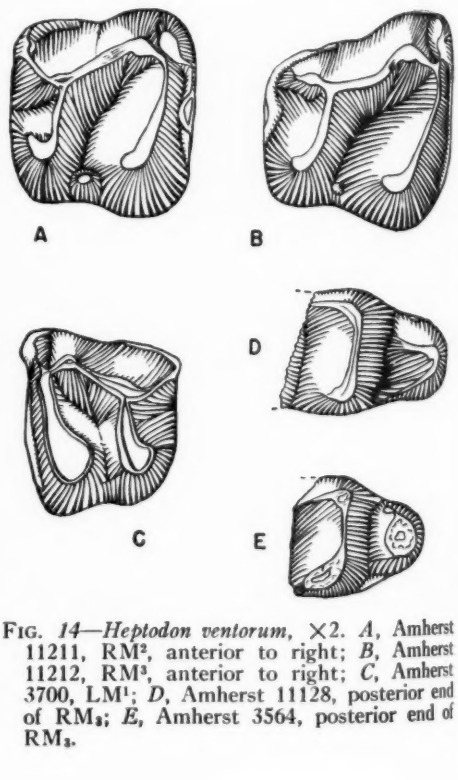

Fig. *14—Heptodon ventorum*, ×2. *A*, Amherst 11211, RM^2, anterior to right; *B*, Amherst 11212, RM^3, anterior to right; *C*, Amherst 3700, LM^1; *D*, Amherst 11128, posterior end of RM_3; *E*, Amherst 3564, posterior end of RM_3.

11212, an M^3, are both considerably larger than the type of *H. ventorum*, and the paracone is poorly separated from the parastyle (fig. 14, A–B). Another tooth, Amherst 3700, an M^1, is approximately the size of the corresponding tooth of the type of *H. ventorum* and has the characteristic high trihedral paracone well separated from the parastyle (fig. 14, C). In the two larger molars there is a small, but well-developed, cusplet between the protocone and hypocone, blocking the lingual opening of the central valley. In M^1 there is merely a faint break in the slope of the lingual end of the valley. Since *H. posticus* is larger than *H. ventorum*, it is possible that the larger upper molars are those of *H. posticus*.

The last lower molars of the two lower jaw fragments are intermediate in size between those of the type of *H. posticus* and the referred specimen of *H. ventorum* (Cope, 1885, pl. 58, fig. 5). The heel of these teeth is narrow with an elongate hypoconulid more similar to the type of *H. posticus* than to *H. ventorum*. This is also seen in a broken M_3 (fig. 14, D). In another broken M_3, the heel is small and the hypoconulid a low, broadly rounded cusp more like the condition in *H. ventorum* (fig. 14, E).

It has been seen from the study of the Amherst *Hyopsodus* and *Hyracotherium* material that such characters as length and width of teeth, development of posterior cusps on P_4, condition of the heel on M_3, and prominence of lophs and cingula, are extremely variable within a species population. These characters are those that have been used in differentiating between species of *Heptodon* (cf. Cope, 1880, 1882 and 1885; Wortman, 1896). What value they have as specific criteria in *Heptodon* is not known, but it has been shown that they must be used with caution. It is possible that *H. posticus* was a large variant of *H. ventorum* inhabiting the Big Horn Basin during the Lysite, as is perhaps the case with *Hyopsodus powellianus powellianus* of the Big Horn Basin and *Hyopsodus powellianus browni* of the Wind River Basin.

Order ARTIODACTYLA
Family DICHOBUNIDAE
WASATCHIA cf. W. DORSEYANA Sinclair, 1914
Figure 15, A

Three isolated third lower molars have been referred to this genus from the Amherst Lysite collections. Van Houten (1945, p. 458) lists only *W. lysitensis* from the Lysite and equivalents. From Sinclair's revision of the Eocene Artiodactyla (1914) there seems to be no basis for the separation of *W. lysitensis* and *W. dorseyana* other than size, the former being somewhat larger than the latter. Size is used as the basis of referring these forms to *W. dorseyana*.

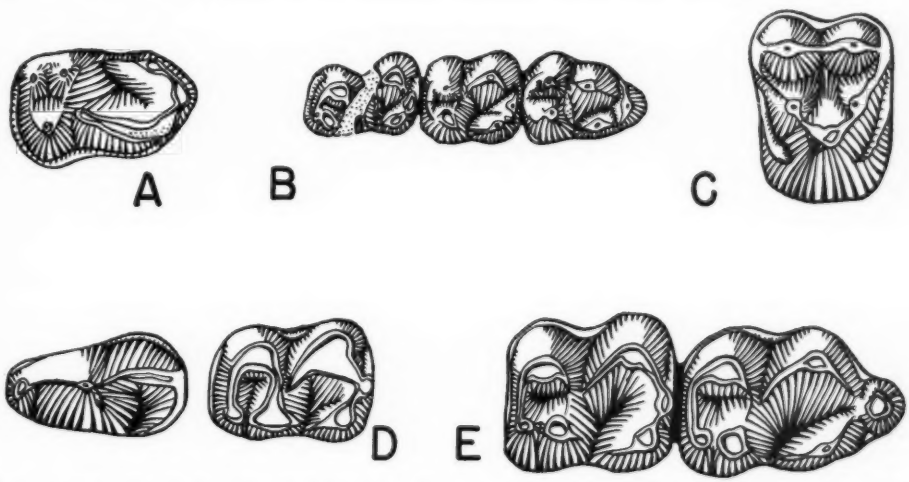

FIG. 15—Teeth of artiodactyls. *A*, *Wasatchia dorseyana*, Amherst 11189, LM_3, ×3; *B*, *Bunophorus macropternus*, Amherst 11103, RM_{1-3}, ×2; *C*, cf. *B. macropternus*, Amherst 11194, RM^1, ×2. Anterior to right; *D*, *Diacodexis chacensis*, Amherst 3528, RP_4–M_1, ×5; *E*, *D. chacensis*, Amherst 11252, RM_{2-3}, ×5.

The measurements of the Amherst specimens indicate that they are referable to *W. dorseyana* and not to *W. lysitensis*. The three third lower molars are almost identical with that of *W. dorseyana* (Sinclair, 1914, fig. 3).

It is peculiar that all specimens previously collected from the type Lysite are referable to *W. lysitensis* and none to *W. dorseyana*, and that the isolated teeth present in the Amherst collections are all referable by size to *W. dorseyana* and not *W. lysitensis*. It seems probable that, in this group of animals, size is not a valid criterion for separating species, and that the two forms are merely size extremes of a single variable species population such as has been determined for other Lysite animals.

Bunophorus macropternus (Cope), 1882
Figure 15, B–C

Three specimens of lower teeth are referred to this little known genus. Two upper molars are questionably referred here. The most complete specimen (Amherst 11103) is a badly weathered fragment of a right jaw with fractured M_{1-3} (fig. 15, B). The second specimen (Amherst 11110) is an isolated LM_1 probably from the same animal as the first specimen, since it was found in the same pocket and is of identical size and stage of wear. The third specimen (Amherst 11204) is an isolated M_2.

There seems to be little difference between the two species of this genus, *B. etsagicus* and *B. macropternus*. The type of *B. etsagicus* has badly worn first and second lower molars but P_{3-4} and M_3 are well preserved. The type of *B. macropternus* has well preserved M_{1-2}, no premolars, and half of M_3 broken off. There thus seems to be little in the way of material common to both for comparison.

Sinclair (1914) gives only the following structural differences between these two species:

B. macropternus	*B. etsagicus*
small paraconid on M_1	?
no paraconid on M_2	?
vestige of paraconid on M_3	no paraconid on M_3
cingula strong, anterior in part external	cingula weak, faint traces externally, faint anteriorly
enamel slightly rugose	enamel smooth

As has been shown above, these types of structural characteristics are exceptionally variable in unspecialized lower Eocene mammal species populations, and are of doubtful value in specific differentiation, merely constituting variations within a population. The Amherst specimens show variations ranging from the characteristics of one species to those of the other. The paraconid is slight on M^1, absent on M_3, and very faint or absent on M_2 (fig. 15, B). The anterior cingulum varies from strong to faint and the enamel is generally smooth. The tooth length of the Amherst specimens is intermediate between that of the holotypes in the two species. In transverse diameter the teeth are closer to *B. macropternus*.

It can be easily seen therefore that it is difficult to assign these specimens to one or the other species with certainty. It is very possible that *B. etsagicus* and *B. macropternus* are not specifically different, but this problem cannot be determined without much more material. Since *B. etsagicus* has not been recorded in the Lysite and *B. macropternus* is characteristic of the Lysite, the Amherst specimens are referred to the latter.

Two upper molars are tentatively referred here as they are of the correct size to belong with the lower teeth. Upper teeth of *Bunophorus* have not previously been figured, and Gazin (1952, p. 73) is the first to have described them, so the reference is somewhat uncertain. The Amherst material agrees with Gazin's description. The teeth differ from those of *Wasatchia* in the very minute size of the hypocone (fig. 15, C), which is merely a cuspule on the posterior cingulum. All the cusps are rounded, and the cingula are large, giving the tooth a nearly rectangular form. Again this is a difference from *Wasatchia*.

Diacodexis chacensis (Cope), 1875
Figure 15, D–E

This is by far the most abundant artio-

dactyl in the Amherst Lysite series, being represented by one M^1, a specimen with P_4-M_1 of both sides, four fragments with M_{2-3}, and six isolated third lower molars. This seems to be the first identification of *Diacodexis* in the Wind River Lysite.

All the lower teeth clearly show the generic feature of a well-developed paraconid; in all the talonid is wider than the trigonid; and in all the heel of M_3 is elongate, with an isolated hypoconulid.

At present, the species can best be separated on the basis of size. On this basis, all of the Amherst specimens are referable to *D. chacensis*.

SUMMARY

The Amherst collection of mammals from the type locality of the Lysite fauna of upper lower Eocene age is studied and reidentified. Twelve forms are recognized for the first time in the fauna, three of them new species.

Statistical studies have been made wherever possible. It is clear that all of the mammals of this period are rather variable in tooth dimensions and in the details of tooth pattern. Wherever an adequate sample is available, it can be shown that the Lysite populations are more variable than is generally considered to be the case with mammalian species, but that a continuous curve of variability is present, and complete intergradation occurs between forms which have been considered distinct species. Where there is not adequate material to permit such studies, there still appears to be similar variability, suggesting that this may be a characteristic feature of the mammals of this period.

In some cases, there appear to have been slight differences between the populations of a given species from the Lysite and contemporaneous populations of the same species from the Big Horn Basin. If studies of material from the latter area should bear this out, these might be considered to be geographic races, even though separated by a relatively short distance.

If additional evidence were needed, this will help to indicate the unreliability of using the holotype of a species as more than a member of the population to which it belongs. Obviously, the holotype has to belong to the species whose name it carries, but it can in no way set limits on the range of variability that occurred within the once-living species of which it was a member.

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QUANTITATIVE STUDIES OF BRACHIOPODS FROM THE LOWER CARBONIFEROUS REEF LIMESTONES OF ENGLAND
I. *SCHIZOPHORIA RESUPINATA* (MARTIN)

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ABSTRACT—A statistical investigation of a large number of specimens of *S. resupinata* from the reef facies of various localities in northern England reveals highly significant differences in shell shape between the *Caninia* zone (C) and *Dibunophyllum* zone (D) populations and less significant differences between assemblages within the D zone. From the lower to the higher stratigraphical level the length /width ratio tends to increase, and there is a still greater increase in the thickness/width ratio, a consequence, it is thought, of phylogenetic change.

Relative growth between the different dimensions is allometric with changes in the growth ratios at a shell width of about 20 mm.

INTRODUCTION

PROMINENT in the Lower Carboniferous of northern England are the mounds of unbedded or obscurely bedded limestone known as reef knolls. The reef facies contains a varied fauna in which brachiopods are the most characteristic and widely distributed forms. A few of the commoner types, including among others *Schizophoria resupinata* (Martin), *Pugnax acuminatus* (J. Sowerby), *P. pugnus* (Martin) and *Camarotoechia pleurodon* (Phillips), have been studied by the author on a statistical basis. This paper is concerned with the first-named species.

Variation in British and Belgian Schizophoriidae has been studied by Bond (1941) who interpreted the common species *S. resupinata* broadly, by including within it the varieties *gigantea*, *dorsisinuata*, *lata*, *pinguis* and *rotundata* Demanet and *elboltonensis* George and Ponsford. The species ranges throughout the Tournaisian and Viséan stages of the Dinantian (Demanet, 1934). Bond was unable with the material at his disposal to detect stratigraphical variation, though he recognized that such variation might be disclosed by the employment of statistical analysis. The internal characters and external ornament of *Schizophoria* have been studied by George and Ponsford (1937) and by Bond (1941). These features do not lend themselves readily to statistical treatment.

The present paper records the results of a quantitative investigation of more than 2,000 specimens, all considered to belong to *S. resupinata*. The author's interpretation of this species, which is the same as that of Bond, is based also on the morphological studies of George and Ponsford, and has been influenced by his own long experience of stratigraphical work in the reef limestones. The statistical analyses are made on measurements of different parts of the shell. The spacing of the costellae (3 to 5 mm. at 1 cm. from the ventral umbo), was also examined, but the precision of measurement was not such as to justify the employment of this feature as a quantitative measure of variation. The author's limited examination of internal characters adds nothing to the observations of George and Ponsford and of Bond. He is reasonably satisfied that he has not made use of specimens superficially resembling *S. resupinata* but with different internal structure.

Much of the precisely localized material is of the author's collecting. Museum specimens have not been used except where the broad stratigraphical level is known.

Acknowledgment.—The author is grateful to many friends for help of various kinds, and particularly to Mr. C. H. Leigh-Dugmore of the Dunlop Rubber Company for his valuable suggestions and expert criticism in the statistical field. The drawing of the neotype (fig. 1) is the work of Mr.

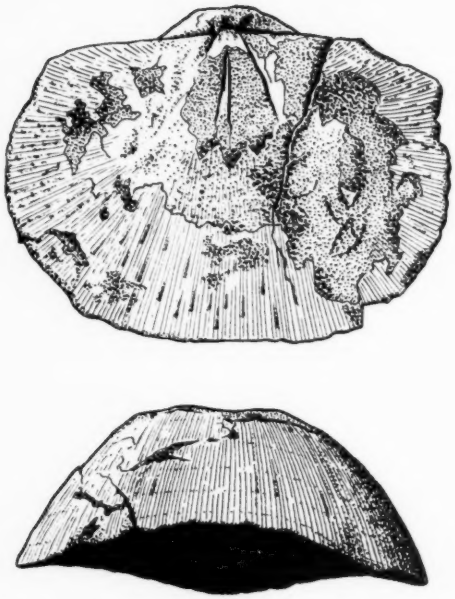

FIG. 1—Neotype of *Schizophoria resupinata* (British Museum Coll. No. BB, 2420) ×¾.

T. E. H. Gray, and all the other diagrams have been made from the author's rough copies by Mr. H. R. Willcocks. For the loan of museum specimens the author is indebted to Dr. A. Raistrick, Mr. Angus Dunn, Dr. C. J. Stubblefield and Dr. H. M. Muir-Wood. He also wishes to thank Mr. J. Ranson, Dr. W. S. Norris, Dr. F. Hodson and Mr. S. Westhead for the loan or gift of material from Withgill and other localities in the neighbourhood of Clitheroe.

STATISTICAL METHODS EMPLOYED IN COMPARING POPULATIONS

In the present study simple quantitative methods only have been applied to the data. For reasons to be given later, the more complex techniques such as multiple regression have not been used. The characters compared are the total width of the shell, W, the total length, L, the length of the brachial valve, L_B, the length of the pedicle valve, L_P, the maximum thickness, T, and (in part) the length of the hinge line. Ratios of the dimensions have also been employed as separate characters.

The illustration of the neotype (fig. 1) is copied from Bond's figure (1941, pl. 21). Two further specimens are figured in outline (fig. 2), one being about average in general characters, and the other a more globose form with a relatively long brachial valve. These diagrams illustrate the terms length, width and thickness, which are those conventionally used for brachiopods, the length being measured in a straight line from the highest point of the umbo to the middle of the anterior margin of the shell, the width being the greatest measurement in a straight line parallel to the hinge line and at right angles to the length, and the thickness the distance through the middle of the shell at right angles to the length and width.

Paleontologists have usually considered that in a given sample unimodal distributions of the different characters, and in particular the ratios of the dimensions, indicate that the sample is representative of a single population. In the present study ratios have been employed for tests of significance between communities. Where relative growth between two characters is not isometric (i.e. where the growth rates are not equal) the value of the ratio (e.g. T/W) is dependent upon the size of the shell, but this does not invalidate its use for discrimination purposes, since the ratio is regarded as a separate character which, though mainly determining shape, is also influenced by size and spread of size. The con-

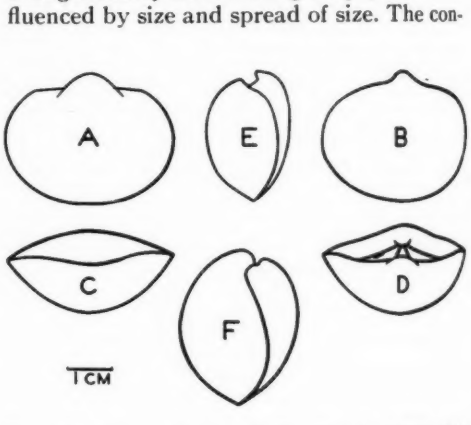

FIG. 2—*S. resupinata*. A–E, Treak Cliff *Dielasma* bed), F, Eldon Hill quarry. A, dorsal view; B, ventral view; C, anterior view; D, posterior view; E, with longer pedicle than brachial valve; F, with longer brachial than pedicle valve.

clusions to be drawn from the tests of significance will, however, be influenced by differences in relative growth rates.

Simple regression analysis, employed primarily for the study of relative growth has also been used, where appropriate, for tests of significance. For the most part, however, growth features have been compared by the reduced major axis method of Kermack and Haldane (1950) which is less cumbersome than regression and avoids describing one variate as independent. The equations derived from the two procedures are closely similar.

The tests of significance employed are Student's "*t*" and where appropriate the variance ratio *F*. Experience has suggested that the probability level of significance should be taken as 1% instead of the more usual 5%.

Tests of significance are valid only for samples randomly drawn from the population in question, and therefore in a number of cases have not been made because of suspected non-randomness. Departures from randomness can arise in different ways, and notably in a collector's tendency to pick up large specimens, which reduces the probability of small specimens being gathered. The statistics of these possible non-random collections are, however, recorded in Table 1, and have not been ignored completely since where differences between collections are sufficiently great it can sometimes be inferred that they are unlikely to come from the same population, although no objective measure is possible of this degree of "unlikeliness."

The deme (Gilmour and Gregor, 1939, and Sylvester-Bradley, 1951) is taken as the unit of population. In some cases the deme might have subspecific rank. These and related matters of classification are discussed later.

COMPARISONS OF THE COLLECTIONS

Without exception the specimens submitted to statistical examination have been obtained either from the *Caninia* zone C_1–C_2, or the *Dibunophyllum* zone D_1–D_2, and they are all from reef limestone. The reef facies is rare in the intervening *Seminula* zone S_1–S_2, which has yielded no measurable specimens and it is unknown below the *C* zone. Brachiopods from "standard" limestone cannot usually be extracted from the matrix and do not lend themselves easily to growth and variation studies. Of the 71 specimens from the *C* zone almost all are from C_2 and most of them from near the top of C_2. The great majority of the 1,987 specimens from the *D* zone are probably from the upper part of D_1. There is thus 28 times the quantity of material available from the *D* than from the *C* reefs. This is not surprising in view of the considerably greater abundance of fossils of all kinds in the *D* than in the *C* reefs.

The first sample to be considered consists of 36 measurable specimens from C_2 of Withgill quarry, a small inlier of reef limestone 3 miles southwest of Clitheroe, Lancashire. The thickness of beds represented can hardly be more than 20 or 30 feet at a level near the top of the Clitheroe Limestone.

The sample of 23 specimens from elsewhere in the Clitheroe Limestone is drawn from various localities in the area Clitheroe-Twiston-Whitewell-Slaidburn which are mostly representative of the higher beds of the C_2 zone, but some belong to older horizons and the collection includes a specimen, indistinguishable from typical C_2 forms, from Coplow Quarry in the upper part of C_1. This assemblage in fact ranges over a considerable thickness of reef limestone (about 1,500 feet) but it does not contain any specimens from beds younger than those of Withgill Quarry.

Table 2, which is based on the data of Table 1, shows that for all the characters measured there is no significant difference between the two samples. It seems reasonable therefore to regard the Withgill collection as typical of the *C* zone of the Clitheroe Bowland area, and it is moreover a completely random sample, precisely localized. For these reasons it is suitable as a standard to represent the *C* zone in comparison with the different samples from the *D* zone. It should be added that a specimen figured by Davidson (1857–62, Plate XXIX, fig. 3) in a private collection and stated to come from Withgill is in its dimension ratios unlike any *S. resupinata* among the very large number examined and the author feels justified in ignoring it.

TABLE 1

W maximum width
L total length
T maximum thickness
L_B length of brachial valve
L_P length of pedicle valve
N number of specimens

All dimensions are in millimeters

Locality		N	Range	Mean	Standard Deviation
Withgill	W	36	16.0 –48.0	32.56	9.134
	L	36	13.1 –37.2	25.06	6.362
	T	36	6.2 –24.0	14.53	4.475
	L/W	36	0.651– 0.850	0.7756	0.0502
	T/W	36	0.355– 0.509	0.4459	0.0362
	T/L	36	0.473– 0.711	0.5803	0.0484
	L_B/L_P	32	0.955– 1.025	0.9942	0.0147
Clitheroe-Slaidburn	L/W	23	0.673– 0.870	0.7806	0.0446
	T/W	23	0.361– 0.545	0.4602	0.0419
	T/L	23	0.505– 0.705	0.5936	0.0523
	L_B/L_P	21	0.930– 1.024	0.9978	0.0188
Little Island, County Cork	L/W	12	0.683– 0.883	0.8237	0.0608
	T/W	12	0.306– 0.558	0.4464	0.0720
	T/L	12	0.449– 0.697	0.5425	0.0794
	L_B/L_P	12	0.96 – 1.01	0.981	0.018
Dielasma bed, Treak Cliff	W	201	7.7 –37.0	16.33	4.867
	L	201	6.0 –29.8	13.39	4.216
	T	201	3.6 –19.2	9.45	3.083
	L/W	201	0.724– 1.000	0.8193	0.045
	T/W	201	0.392– 0.764	0.5553	0.0583
	T/L	201	0.495– 0.878	0.6794	0.0570
	T/L_P	194	0.463– 0.878	0.6954	0.0675
	L_B/L_P	191	0.950– 1.151	1.022	0.0371
Craven Reef Belt	W	1695	5.1 –70.0	13.05	4.584
	D	1696	4.2 –52.0	10.87	3.554
	T	1696	2.9 –27.2	7.39	2.550
	L/W	1697	0.666– 0.985	0.8296	0.0461
	T/W	1699	0.367– 0.815	0.5618	0.0659
	T/L	1700	0.462– 0.947	0.6773	0.0632
	L_B/L_P	1484	0.880– 1.120	0.9954	0.0223
Eldon Hill	L/W	18	0.667– 0.884	0.7804	0.0362
	T/W	18	0.286– 0.665	0.5000	0.1190
	T/L	18	0.355– 0.841	0.6373	0.1431
	L_B/L_P	18	0.983– 1.084	1.0012	0.0247
Park Hill	L/W	16	0.718– 0.920	0.8114	0.0629
	T/W	16	0.424– 0.708	0.5501	0.1009
	T/L	16	0.517– 0.815	0.6726	0.0826
	L_B/L_P	15	0.973– 1.069	1.0045	0.0196
Beresford Dale-Narrowdale-Wetton Hill	W	37	7.0 –63.0	27.07	15.64
	L	37	5.5 –53.0	20.94	12.27
	T	37	3.1 –33.5	12.80	7.620
	L/W	37	0.693– 0.885	0.7813	0.0445
	T/W	37	0.358– 0.596	0.4766	0.0582
	T/L	37	0.465– 0.741	0.6099	0.0584
	L_B/L_P	24	0.96 – 1.05	1.0016	0.0224
Mich Low	W	16	30.0 –69.0	52.88	12.50
	T	16	12.5 –37.0	25.06	7.122
	L/W	16	0.706– 0.840	0.7801	0.0362
	T/W	16	0.417– 0.560	0.4751	0.0391
	T/L	16	0.560– 0.676	0.6045	0.0394
	L_B/L_P	16	0.920– 1.170	1.0176	0.0545

The collection in the British Museum (Natural History) of 12 specimens from C_2 of Little Island, County Cork, shows in some respects what appear to be significant differences from the Withgill collection. It cannot be said whether these differences are real or a consequence of the probable non-randomness of the Irish sample.

The six collections from the *Dibunophyllum* zone are taken from localities in Yorkshire, Derbyshire and Staffordshire. In all, 201 measurable specimens of *Schizophoria resupinata* were collected by the author (with some assistance from students of Sheffield University) from a thin bed on Treak Cliff, near Castleton, Derbyshire. This deposit, which is in reef limestone immediately below the summit ridge, has been referred to (Parkinson, 1952) as the *Dielasma* bed. It is an extremely fossiliferous pocket about a foot thick and a few feet in length in the D_1 zone and immediately below beds with a sparse fauna, including *Dibunophyllum bourtonense* Garwood and Goodyear and *Davidsonina septosa* (Phillips) which is representative of high middle D_1. The *Dielasma* bed community will now be compared with collections from the D zone of various localities.

The specimens from the Craven Reef belt, of D_1-lower D_2 age are not precisely localized. With a few exceptions they belong to the Tiddman collection in the Skipton Museum and were collected in the area between Settle and Greenhow in Yorkshire. The writer agrees with Bond (1941) that they should all be referred to *S. resupinata*. Since the Craven Reef limestone is a few hundred feet thick the objection might be raised that the collection is a composite one including specimens from different horizons and therefore unsuited to statistical treatment. However, experience to date has not suggested any marked change in the brachiopod faunas in general within the confines of the D_1–D_2 reef limestone. Furthermore, the sample examined is a large one, including more than 2,000 individuals of which 1,700 are sufficiently well preserved for statistical investigation. It can be taken as a random sample representative of the Craven Reef belt as a whole, and as such can be compared with samples from other areas, whether from beds of the same or of different age. It seems probable that the great majority of the specimens came from beds above lower D_1. Bond (1950) has in fact shown that the richly fossiliferous brachiopod beds of the Cracoe reef limestones, which include the most extensive collecting grounds of the Craven Reef belt are confined to the middle and upper parts of D_1 and the lower part of D_2. The *Dielasma* bed of Treak Cliff occupies a narrow horizon within this broad zone.

TABLE 2.—SIGNIFICANCE OF DIFFERENCES BETWEEN RATIOS

S = significant at 1% level of probability
N.S. = not significant

Comparison	Ratio	Means	Variances
Withgill and Clitheroe-Slaidburn	L/W	N.S.	N.S.
	T/W	N.S.	N.S.
	T/L	N.S.	N.S.
	L_B/L_P	N.S.	N.S.
Dielasma bed and Craven Reef Belt	L/W	S.	N.S.
	T/W	N.S.	N.S.
	T/L	N.S.	N.S.
	L_B/L_P	S.	S.
Withgill and *Dielasma* bed	L/W	S.	N.S.
	T/W	S.	S.
	T/L	S.	N.S.
	L_B/L_P	S.	S.
Withgill and Craven Reef Belt	L/W	S.	N.S.
	T/W	S.	S.
	T/L	S.	N.S.
	L_B/L_P	N.S.	S.

Comparison of the different characters (Tables 1 and 2) has shown certain significant differences between the Treak Cliff and Craven Reef assemblages. The size measurements indicate larger means for the former than for the latter sample. As regards the dimensions ratios, the distributions of which are illustrated by the histograms of figure 3, tests of significance (Table 2) indicate no difference between the samples in T/W and T/L but significant differences in the L/W ratio of the shell and in the relative lengths of the two valves. Most of the specimens from the *Dielasma* bed have a longer brachial than pedicle valve, in contrast to the more usual longer pedicle valve in the Craven Reef sample.

One and a half miles south-west of Treak Cliff is Eldon Hill Quarry of upper (or upper

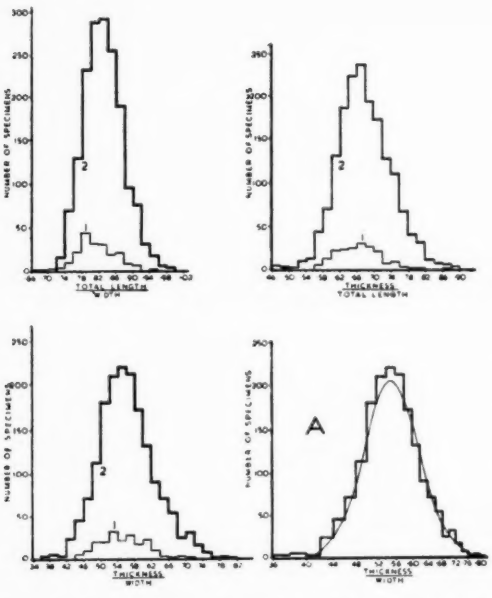

FIG. 3—Histograms illustrating distributions of the different ratios of specimens from (1) *Dielasma* bed, Treak Cliff and (2) Craven Reef Belt. In Figure 3A the abscissae are on a logarithmic scale and the smooth superimposed curve is the normal Gaussian.

middle) D_1 age. The sample of 18 specimens is drawn from a thickness of some 50 feet of strata and cannot be regarded as a random one. An interesting feature of this collection is the wide range in the T/W and T/L ratios and the greater variances than those of the *Dielasma* bed community.

The sample in the Geological Survey museum of 16 specimens from the D zone of Park Hill, Derbyshire, which shows points of difference from the *Dielasma* bed sample is probably non-random.

The 37 specimens from D_1 (with probably some from lower D_2) of the area Beresford Dale-Narrowdale-Wetton Hill of Derbyshire and North Staffordshire constitute a combined (though probably not random) sample from the Natural History and Geological Survey museums. In the means of all characters it is apparently different from the *Dielasma* bed sample.

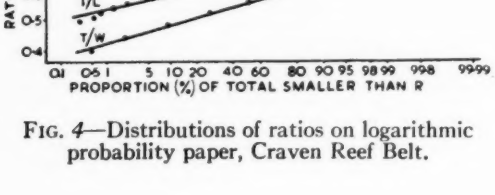

FIG. 4—Distributions of ratios on logarithmic probability paper, Craven Reef Belt.

The reef limestone of Mich Low, near Bradwell, Derbyshire, probably represents a higher horizon than any so far considered. It is thought to be of lower D_2 age (Parkinson, 1947). The sample of 16 specimens was obtained by a quarryman from an excavation and is unlikely to be a random one since it contains only large individuals. It differs in all characters from the *Dielasma* bed collection.

Except in figure 5 where the Withgill collection is combined with the Clitheroe-Slaidburn collection to form a composite sample, Withgill is taken as the standard for the C reefs in comparison with samples from the D reefs, for the reasons already given. The data show it to differ significantly and in most respects highly significantly from both the *Dielasma* bed and Craven

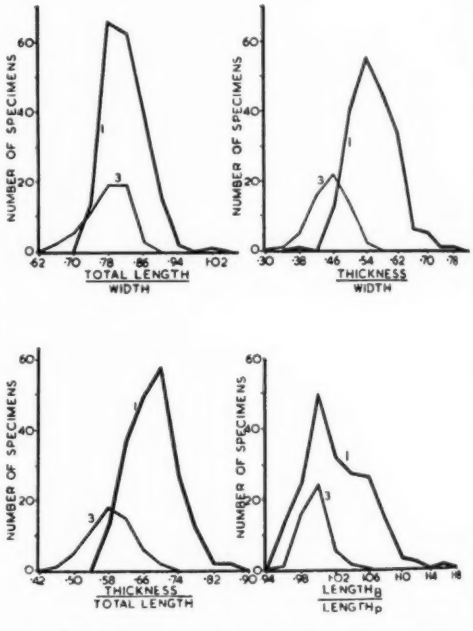

FIG. 5—Frequency polygons illustrating distributions of the different ratios of specimens from (1) *Dielasma* bed, Treak Cliff, (3) Withgill and Clitheroe-Slaidburn.

Reef samples. The *Dielasma* bed community (except for the L_B/L_P ratio which is unusually high) may be regarded as characteristic of the *D* zone and the frequency polygons of figure 5 serve to show at a glance the striking differences existing between typical samples from the *C* and *D* zones, a difference which is obviously of a much higher order than those within the *D* zone itself.

The greatest differences between the average characters of *C* zone and *D* zone specimens are in the T/W and T/L ratios. Thus the mean T/W ratio for 71 specimens from the *C* zone is 0.4506 and that for the *D* zone is 0.5582; the corresponding T/L ratios are 0.5721 and 0.6468, respectively, whilst those of L/W are 0.7868 and 0.8261. There is no marked general tendency for the L_B/L_P ratio to be higher in the younger than the older beds, the high value for the *Dielasma* bed sample having apparently no more than local significance.

GROWTH FEATURES

Scatter diagrams relating length to width in *S. resupinata* indicate approximate isometric growth (Parkinson, 1952), i.e. the growth rates are equal and the two variables

TABLE 3.—EQUATIONS EXPRESSING RELATIONS BETWEEN THE DIMENSIONS

W=width L=total width T=thickness

Withgill	
$L=1.064\ W^{0.908}$	$\log L=0.908 \log W+0.027$
$T=0.325\ W^{1.090}$	$\log T=1.090 \log W-0.488$
$T=0.300\ L^{1.202}$	$\log T=1.202 \log L-0.523$
Dielasma *Bed, Treak Cliff*	
$L=0.850\ W-0.48$	
$L=0.777\ W^{1.019}$	$\log L=1.019 \log W-0.109$
$T=0.411\ W^{1.110}$	$\log T=1.110 \log W-0.386$
$T=0.568\ L^{1.070}$	$\log T=1.070 \log L-0.246$
Craven Reef Belt. All sizes	
$L=0.777\ W+0.67$	
$W<20$ mm.	
$L=0.765\ W^{1.032}$	$\log L=1.032 \log W-0.116$
$T=0.318\ W^{1.225}$	$\log T=1.225 \log W-0.498$
$T=0.392\ L^{1.234}$	$\log T=1.234 \log L-0.407$
$W>20$ mm.	
$L=0.764\ W^{1.010}$	$\log L=1.010 \log W=0.117$
$T=0.754\ W^{0.888}$	$\log T=0.888 \log W-0.123$
$T=0.892\ L^{0.901}$	$\log T=0.901 \log L-0.050$

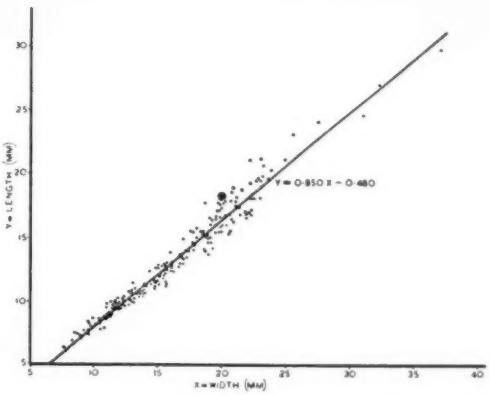

FIG. 6—Relation of length to width, *Dielasma* bed, Treak Cliff.

are linearly related. One such diagram is reproduced—that of the *Dielasma* bed (fig. 6). The equation of the regression line (fig. 6 and Table 3), was determined in the usual way by the method of least squares, the width being taken as the independent variate and hence as a measure of the age of the individual. The writer (1952) has given reasons for the choice of width as a measure of age in the case of the brachiopod *Dielasma hastata*. The regression line does not quite pass through the origin of the graph as would be expected for truly isometric growth throughout life, but the intercept is not significant.

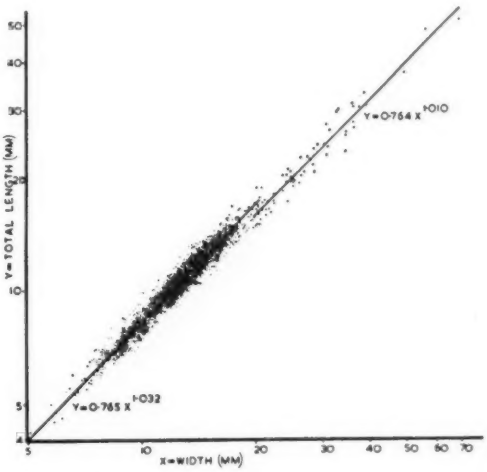

FIG. 7—Relation of length to width on log/log scale, Craven Reef Belt.

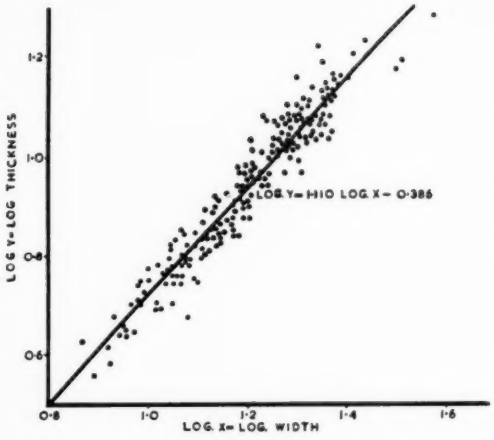

FIG. 8—Relation of log thickness to log width, *Dielasma* bed, Treak Cliff.

The corresponding regression equation relating length to width for the Craven Reef sample is given in Table 3. It differs significantly from the *Dielasma* bed equation, thus providing additional evidence that the two samples should be regarded as belonging to different populations.

Although a length-width plot of the Craven Reef specimens (not reproduced here) indicates an approximate isometric relation a straight line could not be drawn centrally through all the points and therefore a graph was produced on a double logarithmic scale (fig. 7). The scatter of the points up to a width of about 20 mm. forms a dense cloud elongated linearly and indicating that the growth relationship is in reality allometric rather than isometric, i.e., the growth rates maintain a constant ratio. (The exponent in the allometric equation is a measure of this ratio and gives the slope of the regression line. Isometric growth is a special case when the ratio = 1. See Parkinson, 1952, for a fuller explanation.) Relative growth is considered at length in Zuckerman and others (1951).

The data were handled not by regression analysis but by the method of Kermack and Haldane (1950), the specimens of breadth greater than 20 mm. being analyzed separately. It is seen from figure 7 that the lines pass centrally through the points and indicate a small decrease in the growth ratio at 20 mm. or thereabouts, as shown by a change in slope from 1.032 to 1.010.

In the case of the thickness-width and thickness-length arithmetical plots curvilinear relations were found for all samples studied. These graphs are not reproduced in the paper. Allometry was tested in some cases by arithmetical plots of the logarithms of the dimensions and in others by plotting the actual dimensions on log/log paper. In Table 3 both the exponential and logarithmic forms of the allometric equations are recorded. Simple allometry is indicated for the *Dielasma* bed samples (figs. 8 and 9), there being no obvious change in slope in either the log T—log W or log T log L plots. However, as there seem to be no really large specimens in this community a change in the slope of the line at the expected position (20 mm. width) might in fact exist without being easily detected.

In figure 10 T is plotted against W of the specimens from the Craven Reef Belt on a double logarithmic scale and Kermack and Haldane's procedure applied separately to the specimens greater and less than 20 mm. wide. Growth is seen to be allometric with a pronounced change in the ratio (slope of the lines) which is greater than unity in the early stages and less than unity in the late stages. Figure 11 shows a similar allometric relation in two stages, between the thickness and the length.

Plots of the logarithms of L against W, T against W and T against L of the Withgill

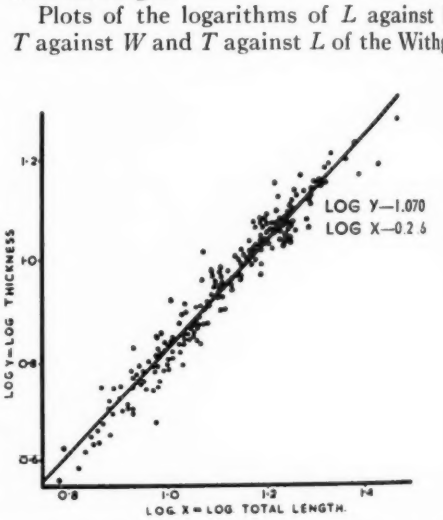

FIG. 9—Relation of log thickness to log length, *Dielasma* bed, Treak Cliff.

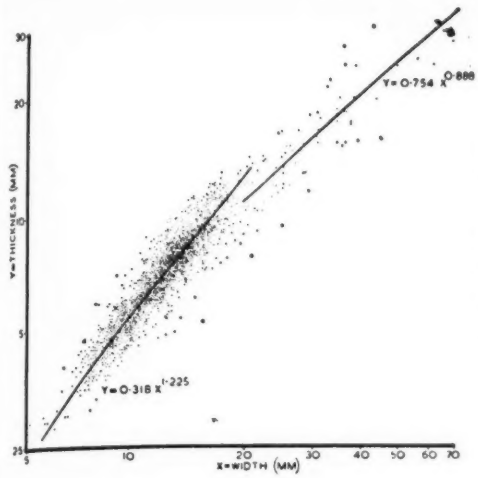

FIG. *10*—Relation of thickness to width on log/log scale, Craven Reef Belt.

specimens are drawn in figures 12, 13 and 14 and the Kermack and Haldane line shows an allometric relation in each. Since the sample is a relatively small one with very few individuals having a width of less than 20 mm. any change in growth that might have occurred thereabouts cannot be proved. The broken lines on each graph represent the corresponding equations of the *Dielasma* bed sample and it is immediately evident that the differences between the samples are great.

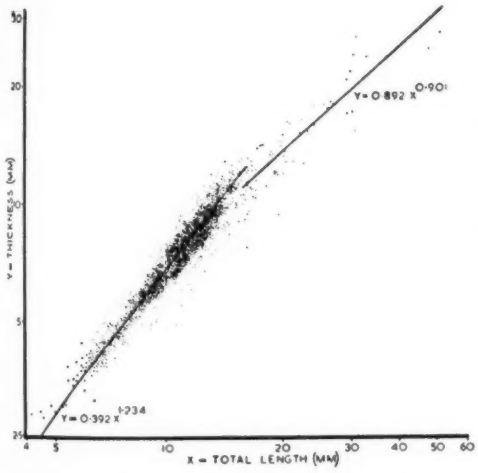

FIG. *11*—Relation of thickness to length on log/log scale, Craven Reef Belt.

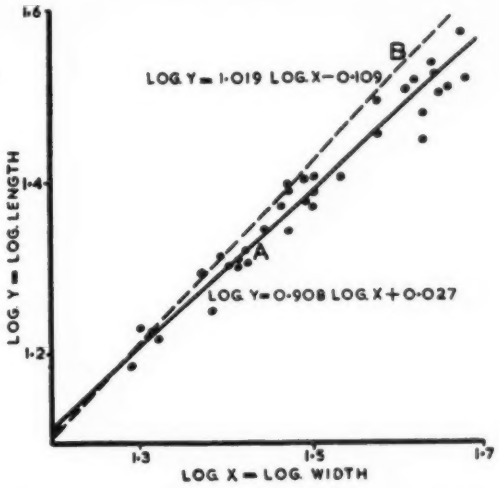

FIG. *12*—Relation of log length to log width. Full line and scatter, Withgill; broken line, *Dielasma* bed, Treak Cliff.

The change in the growth ratios at a width of about 20 mm. provides an interesting parallel with *Dielasma hastata* from Treak Cliff (Parkinson, 1952). This brachiopod also shows two distinct growth stages, the change taking place curiously enough at approximately the same width.

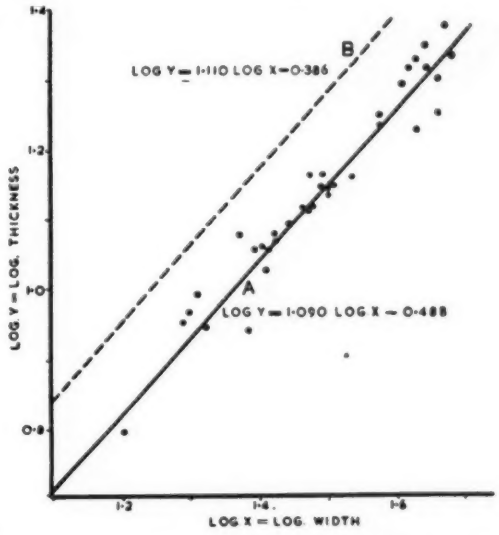

FIG. *13*—Relation of log thickness to log width. Full line and scatter, Withgill; broken line, *Dielasma* bed, Treak Cliff.

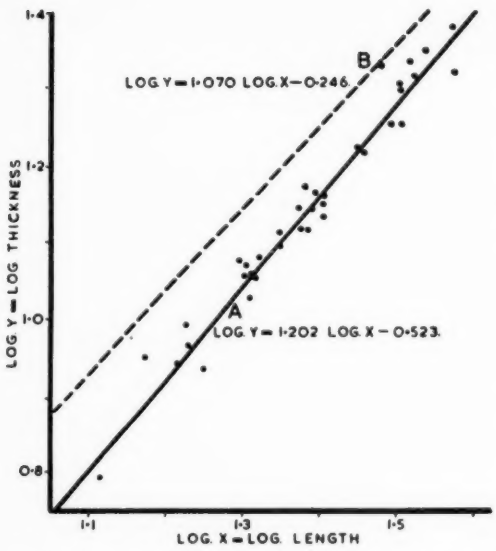

FIG. *14*—Relation of log thickness to log length. Full line and scatter, Withgill; broken line, *Dielasma* bed, Treak Cliff.

A feature of interest relates to the relative thickness of the specimens of varying size. The change in the growth ratio of the Craven Reef specimens means that the larger individuals will tend to be less globose on the average than the ones of intermediate size. There are, in fact, no really inflated specimens (e.g., var. *pinguis*) among the largest shells in any of the samples examined. Similarly there are no globose individuals among the smallest shells. Since the major difference between the *C* and *D* zone form of the species lies in the extent of globosity of the shell it is important to note that what appears to be an evolutionary trend towards increased obesity is not shown either in immature or very old individuals.

It remains to consider how the growth of the hinge line is related to the width of the shell. It soon became evident that with the larger individuals the hinge line increased in length more rapidly as the shell increased in size than if the relation were an allometric one, although for widths of shell up to about 40 mm. it appeared to be approximately allometric (fig. 15 a). It was thought from mechanical considerations that the hinge length might be related to the area of the shell, and therefore a diagram was drawn relating length of hinge to the product of the total length and width (fig. 15 b). The early curved portion of the scatter corresponds approximately to the straight (allometric) portion of figure 15a. The data of figure 15 are taken indiscriminately from the various samples; they indicate that for shells of width greater than 40 mm. the length of the hinge line is approximately linearly related to the area of the shell.

SOME ASPECTS OF VARIATION

The sample of 1,700 specimens from the Craven Reef Belt can be assumed to give precise information on the distribution of the characters of the population from which it is drawn. The frequency distributions of the different dimensions are not figured, though the ranges, means and standard deviations are recorded in Table 1. Each dimension shows a lognormal distribution over the lower part of the range, but with a long flattened tail caused by the comparatively small numbers in the larger size groups. The ratios L/W, T/W and T/L are all distributed lognormally. In figure 3*A* the T/W histogram is drawn on logarithmic abscissae with the normal (Gaussian) curve superimposed. The fit is seen to be almost exact. Plotting the values of this and other ratios on log. probability paper (fig. 4) gives straight lines, indicating lognormality. Simi-

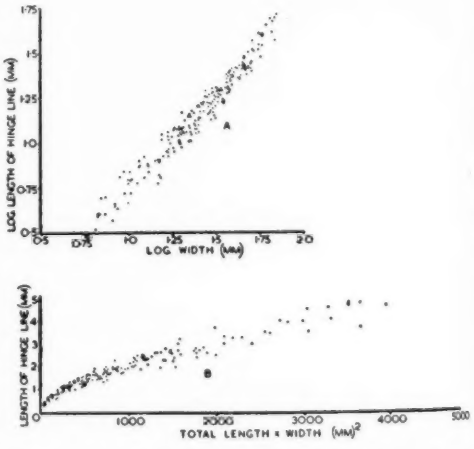

FIG. *15*—(A) Relation of log length of hinge line to log width of shell; (B) relation of length of hinge line to length × width (approx. proportional to area) of shell.

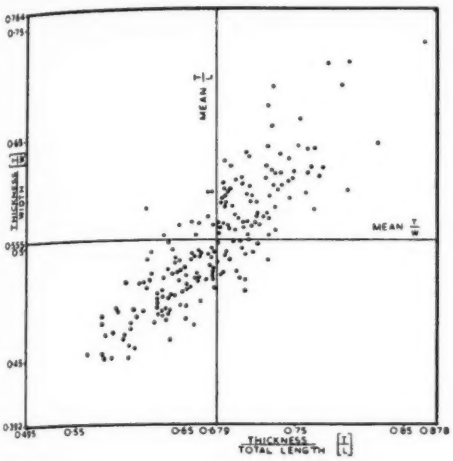

FIG. *16*—Illustrates correlation of length and width at all thicknesses. *Dielasma* bed, Treak Cliff.

lar plots (not figured) of the ratios of the *Dielasma* bed sample of 201 specimens are substantially linear. This tendency towards lognormality is a justification of the use of Kermack and Haldane's shorter method of analysis.

The different ratios of the specimens constituting the *Dielasma* bed sample have been plotted against each other in order to illustrate the degree of dependence existing between the variables. Figure 16 indicates a fairly high correlation between L and W at all thicknesses, most of the points of the scatter lying in opposite quadrants. Correlation is less between L and T (fig. 17) and is substantially non-existent between W and T (fig. 18) which means that at all lengths width and thickness vary independently. These results show a close parallelism with those obtained by the author on *Dielasma hastata* (Parkinson, 1952) and on other brachiopods, and the possibility that they illustrate a general principle in brachiopods should be borne in mind. In this respect it is interesting to note in a variation study of *Pugnax pugnus* B. Simpson (1933) found high correlation between length and width and low correlation between length and thickness.

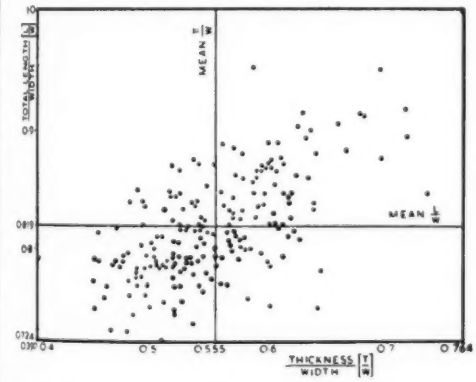

FIG. *17*—Illustrates some degree of correlation between length and thickness at all widths. *Dielasma* bed, Treak Cliff.

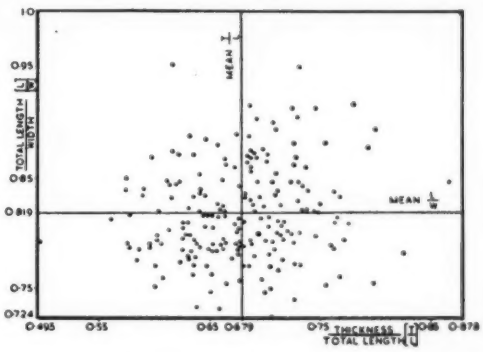

FIG. *18*—Illustrates absence of correlation between width and thickness at all lengths. *Dielasma* bed, Treak Cliff.

Bond (1941) has commented on the tendency of some individuals of *Schizophoria* "to attain an unusual obesity, mainly as a result of increased height [length] of the dorsal valve." This suggests a possible general dependence of the globosity of the shell on the ratio (L_B/L_P) of the lengths of the two valves and figure 19 does indicate a limited correlation of this nature.

DEMES, SUBSPECIES AND HYPODIGMS

In a paper designed to justify the adoption of the chronological subspecies in paleontology Sylvester-Bradley (1951) rightly bases his argument on the assumption that the taxonomic unit is not the individual but the interbreeding population or deme (Gilmour and Gregor, 1939), and points out that a "species is made up of any number of demes, usually isolated from each other by some geographical barrier. Such

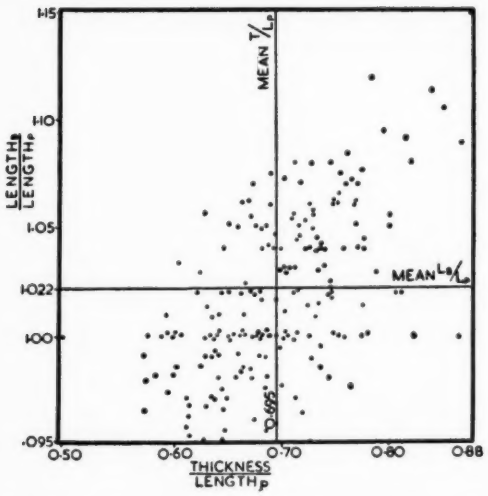

FIG. *19*—Illustrates limited dependence of globosity of shell on the ratio (L_B/L_P) of the lengths of the two valves. *Dielasma* bed, Treak Cliff.

geographically distinct populations are spoken of as topodemes." He proposed the term *chronodeme* to distinguish populations separated in time irrespective of any morphological changes. Thus the approximately synchronous populations of Treak Cliff (*Dielasma* bed) and Eldon Hill, though separated by less than two miles, would be regarded as two topodemes of *S. resupinata*, whereas the Withgill and Treak Cliff populations would rank as chronodemes of the same species. According to Sylvester-Bradley they should also be classed as chronological subspecies since they have been shown to be statistically distinct. The writer considers that Bradley has made out a good case in favour of the subspecies but he suggests that the proposed formula to define the sub-specific unit is inadequate to meet all cases.

This formula is $M \pm 2\sigma_M$, where $\sigma_M = \sigma/\sqrt{N}$, σ is the standard deviation "of any convenient metrical character, M its mean value and N the largest convenient random sample available." The writer agrees that where only one sample is available to estimate σ the formula provides a useful first approximation in the delimination of a population (though, as will be seen, not necessarily of a subspecies). The value of this expression of course depends on the sizes of the samples and it is evident that for a valid comparison of two samples the statistics of both should be taken into account as has been done in the present paper. The writer would mention further that because he has in general found it desirable to work on the 1% level of significance he would prefer to see the "2" in Sylvester-Bradley's formula replaced by "2.6."

A further point arises in this connection. In the present study the variances have been compared as well as the means. Although tests of significance of the means also take the variances into account, cases arise when the means do not differ significantly but the variances do, and in such instances the two samples would be regarded as drawn from different populations.

The question now arises as to whether we can regard our population unit as a measure of the subspecific unit as suggested by Sylvester-Bradley. In the case of *S. resupinata* it would seem desirable for stratigraphical purposes to adopt two subspecies, one for the *C* zone and the other for the *D* zone. Since there are several populations in the *D* reefs at approximately the same horizon, which do we use to define our chronological subspecies? It is not considered to be statistically valid to group those populations that are significantly different from each other (and which can be regarded as approximating to geographical subspecies) into one mixed population.

We can, however, if we define our subspecies more widely, make it comprise a number of nearly related populations. And this brings us to G. G. Simpson's concept of the hypodigm (1940) which is a sample comprising all the specimens studied by an author on which he bases his new species, subspecies and variety. On revision the hypodigm might change in composition as new specimens are added to it or original specimens are taken from it. The hypodigm might be a population sample in the strict statistical sense, or it might be sample drawn from closely related communities. Newell points out (1947, 1949) that a population does not have time duration and that (1949) "only under closely limiting conditions can a hypodigm of fossils be restricted to specimens from a single population." With regard to the subspecies Newell states that unlike a population it does have time

duration and "is composed of a succession of gradually changing populations."

The author's work on this and other brachiopod species provides support for the introduction of the hypodigm into paleontology. But difficulties of nomenclature arise in applying the concept in the present instance, unless the hypodigm is made sufficiently wide to embrace all the specimens considered in the paper, together with the neotype. It would be of more value to stratigraphers if two separate hypodigms, bearing different subspecific names, could be erected, one for the *C* zone and the other for the *D* zone. The neotype of *S. resupinata* comes from an unknown locality in Bolland on the borders of Lancashire and Yorkshire, and although it is highly probably a *C* zone form, its exact level is uncertain. It is a typical representative of the *C* zone hypodigm which could be entitled *S. resupinata resupinata*. A new subspecific name would then be needed for the *D* zone hypodigm; but the author understands that such a procedure would be invalid according to the Rules of the International Commission on Zoological Nomenclature. The writer hesitates to provide and describe two new holotypes which would differ only in shape, the main distinction being the greater thickness in relation to length and width of the higher than the lower form.

Whether or not we try to subdivide the species *S. resupinata* into two subspecies on a time basis we have to recognize the fact that many specimens from the two levels cannot be told apart, and this raises the question of the relation to stratigraphy of the different named varieties of the species. Most of these varieties are found at all levels in the Lower Carboniferous. The gibbous variety *S. r. pinguis* however, seems to be confined both in England and Belgium (Demanet, 1934) to the higher zones of the Dinantian and has some value as an approximate horizon marker. In its T/W and T/L ratios it is of course within the limits of the *D* zone hypodigm, but it comes outside the limits of the *C* zone hypodigm.

MULTIVARIATE ANALYSES

The methods of analysis employed in the present study are simple, if laborious. It is thought that no advantage would have been gained by the use of more complex techniques in this particular case. The method of multiple regression which was adopted by Leitch (1940) for subdividing Coal Measure non-marine lamellibranchs compares several variables at the same time and relates them in a single equation which has value in the diagnosis of the species or subspecies. The method as employed by Leitch assumes that the variables are all linearly related, or that growth is isometric with the growth ratios unchanged throughout life, a condition which probably rarely exists, though the departures from it in some cases are small. This technique is applicable to allometric growth, provided the analysis is made on the logarithms, but again it takes no account of changes in slope of the regression lines and such changes cannot usually be detected unless the sample is large and includes a wide range of sizes. Multiple regression therefore, though a valuable tool, should be used with caution since in some cases it might lead to unsound conclusions.

Other forms of multiple analysis seem to have been little used in paleontology. A type of multivariate analysis was employed by Burma (1949) on blastoids and the present author, in unpublished work on *Pugnax* has investigated the possibilities of the discriminant function technique.

It seems to the writer that simple analyses (pairs of characters at a time) of the type discussed here are in the present state of knowledge more informative in determining the details of ontogeny and phylogeny than the more complex techniques in which such details are obscured in the overall picture. There seems no point, if relations between characters are being studied for their own sake, in extending the analysis to the multivariate approach unless it seems likely that the relationship so obtained can be given reasonable and useful physical explanations. If simple analyses show up significant differences multivariate analyses can do no more at a far greater cost in computation. (See also Olson and Miller, 1951.)

CONCLUSIONS

The following deductions can be drawn from this analysis:

1. Within the *C* zone of the Clitheroe area differences between collections are insignificant.

2. Significant differences are found between communites within the *D* zone.
3. Differences of a higher order of significance than those within the *D* zone are found between the *C* and *D* zone assemblages, suggesting phylogenetic change.
4. Relative growth between different parts of the shell is allometric with a change in the growth ratio at a width of about 20 mm. This change can only be demonstrated with certainty in the case of the large Craven Reef collection. The departure from isometry is very small for the L/W ratios.
5. There is no tendency to increasing size from the lower to the higher stratigraphical levels.
6. The distributions of all dimensions and ratios are unimodal.
7. The distributions of the ratios L/W, T/W and T/L are lognormal. (This is not generally true of brachiopods.)
8. In large specimens the length of the hinge line is roughly proportional to the area of the shell.

The most obvious difference between the *C* zone and *D* zone assemblages is the greater tendency to globosity at the higher level. This is shown from the data of Table 1 which in addition to the English samples include a small collection from C_2 of County Cork, Eire. The latter like the former contains no inflated specimens and none has been noted by the writer among the few specimens collected from the reef facies of the *C* zone of Derbyshire and Staffordshire, nor (as far as memory serves) among the discarded material from these communities and from the *C* zone of Lancashire and Yorkshire. Moreover, in Belgium the gibbous variety *S. r. pinguis* is recorded by Demanet from the *V3b* zone only, near the top of the Viséan.

On the whole the evidence suggests an evolutionary trend towards a greater variety in shape and greater obesity at the higher than the lower level. If this is right the magnitude of the phylogenetic change is indicated by the present study. Thus, the statistical data tell us that between the top of the C_2 zone and the top of the D_1 zone the mean of the T/W ratio has moved through approximately three standard deviations as judged by this value at the Withgill level, and the mean of the T/L ratio through two standard deviations. The corresponding change in the L/W ratio is one standard deviation. This would provide some measure of the rate of evolution (Haldane, 1949) if we knew the duration in millions of years of the *Seminula* and lower *Dibunophyllum* zones. At lower stratigraphical levels than those considered in this study the available data are insufficient to demonstrate phylogenetic change, assuming any to have taken place.

No attempt has been made in this paper to explain the statistical differences between the synchronous populations or topodemes. The subject has been discussed within recent years by Burma (1948) and Sylvester-Bradley (1951) among others, and will not be considered in detail here. Although all the communities of *S. resupinata* under review presumably lived on reef-like structures their environment would change according to such factors as depth of water and position on the reef in relation to basin and massif. Treak Cliff, for instance, is situated on the side of the marginal reef nearest the basin, while Eldon Hill, $1\frac{1}{2}$ miles away is transitional between reef and massif (Parkinson, 1943). Furthermore, isolation of a community could have caused significant modification to structure and may have been a factor in some cases.

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CLASSIFICATION OF AMERICAN DUCK-BILLED DINOSAURS

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ABSTRACT—Sixteen genera of North American duck-billed dinosaurs are referred to two subfamilies, Hadrosaurinae and Lambeosaurinae, of the Hadrosauridae. It is suggested that the subfamilies Saurolophinae and Cheneosaurinae are not based on fundamentally distinct features and should be abandoned.

THE North American Upper Cretaceous duck-billed dinosaurs, Hadrosauridae, have been divided into four subfamilies, i.e. Hadrosaurinae, Saurolophinae, Lambeosaurinae and Cheneosaurinae (Lull and Wright, 1942), but it is believed that a more nearly correct picture would be had if they were classified under two subfamilies, Hadrosaurinae and Lambeosaurinae. The Hadrosaurinae would include those forms in which the premaxillae and nasals were in their normal position, in the front of the head, and were not modified to surround elongated, looped narial passages and the ischium did not terminate in an expanded end. Most of these have been referred to as flat-headed duck-bills. The Lambeosaurinae would include those forms in which the premaxillae were extended and modified to surround elongated, looped narial passages and the nasals were pushed back and up over the frontals. In all of these the ischium terminated in a foot-like expansion. These are popularly referred to as hooded duck-bills.

When Brown described *Saurolophus*, which he called a crested dinosaur (Brown, 1912), he identified the spike-like crest as being composed of nasals, prefrontals, and frontals. When the hooded forms were first described, it was believed that the hood was simply an ornament and was composed of the same bones as the spike of *Saurolophus*. Thus all were classified under the subfamily Saurolophinae (Brown, 1914). Brown believed that the incipient crest of *Prosaurolophus*, a direct ancestor of *Saurolophus*, was also composed of nasals, prefrontals and frontals (Brown, 1916). However, further study of this genus and of *Saurolophus* (Lambe, 1920), (Lull and Wright, 1942) has shown that the spike is an extension of the nasals only, although it is supported by the frontals. The same condition prevails in *Brachylophosaurus*, a recently described form (Sternberg, 1953). Although this spike is a backward extension of the nasals, it has nothing to do with the narial passages, and the premaxillae are confined to the front of the head and do not surround the narial passages. Likewise, the arched nasals of *Kritosaurus* and *Gryposaurus* are in no way related to the development of the hood in the Lambeosaurinae.

The characters given by Brown (1914, p. 565) to define the Saurolophinae were "Skull with crest. Ischium terminating in an expanded foot-like end." The skeleton of Brown's type of *Saurolophus* was rather badly crushed and the distal half of the ischium was not preserved but he associated with it, as plesiotype, a complete ischium (A.M.N.H. No. 5225), which had a foot-like expansion at the distal end. A short time later Brown (1913a) described, as *Hypacrosaurus altispinus*, a new genus and species of hadrosaur from the same beds that yielded *Saurolophus*. The ischium of *Hypacrosaurus* was footed and this genus is now known to be a hooded form (Gilmore, 1924). In 1924 Parks described a fine skeleton of *Prosaurolophus* in which the distal end of the ischium was not footed. As *Prosaurolophus* was closely related to *Saurolophus* and it had a nonfooted ischium, it would appear that the footed ischium that Brown associated with *Saurolophus* probably belonged to *Hypacrosaurus* or some other hooded form.

As there does not appear to be any fundamental character in *Saurolophus* which would justify separating it from the subfamily Hadrosaurinae, I would suggest that the subfamily Saurolophinae be abandoned and that *Saurolophus* and *Prosaurolophus* be classified under the Hadrosaurinae.

Lambe was the first to point out that the hood of *Lambeosaurus* (called *Stephanosaurus*) was composed of premaxillae and nasals and that these bones surrounded the elongated, looped narial passages. The great modification and backward extension of the premaxillae relegated the nasals to the pos-

terosuperior part of the skull and greatly shortened the frontals. The fundamental characters of the hooded hadrosaurs, the Lambeosaurinae, are: muzzle flat, anterior end never reflected; premaxillae greatly extended and folded to surround the elongated, looped narial tubes; frontals shortened and excluded from the orbital rim; maxillae and dentaries short; fang of dentary teeth not forming obtuse angle with enamel crown; ischium with foot-like expansion of distal end; radius usually longer than humerus. The number of tooth rows in the jaws is not dependable because in all hadrosaurs there are fewer tooth rows in younger individuals.

In *Parosaurolophus* the narial passage enters the upper limb of the premaxilla and runs to the back of the elongated hood, then loops down and forward. In *Corythosaurus* and *Tetragonosaurus* and probably in *Cheneosaurus* the narial tube enters the lower limb of the premaxilla and extends back to opposite the orbit, then runs to the upper limb through an S-shaped tube and continues, in this limb, to the top of the hood where it meets the nasal, and the two tubes unite and are surrounded by the nasals to the internal nares. In *Lambeosaurus* the tube runs in the lower limb back to above the orbit, then up in the forwardly bent hood where it meets the nasal and turns sharply downward (Lambe, 1920). Whether the hood is elongated, bent forward, erect and over the posterior part of the cranium or low and far forward, it is made up of the premaxillae and nasals enclosing the looped narial passages. It is never a thin cockscomb, as some early restorations showed, but in some cases there is a thin edge above the expanded hood.

Lull and Wright (1942, p. 178) have proposed the subfamily Cheneosaurinae to include *Tetragonosaurus* and *Cheneosaurus* but it does not seem to me that fundamental differences between these genera and other hooded hadrosaurs are sufficient to justify their separation into distinct subfamilies. In *Cheneosaurus* and *Tetragonosaurus* the hood is much lower and farther foward but this is only a matter of degree for the same bones serve the same functions in all the hooded forms.

The position of *Claosaurus* is uncertain, so it is not considered here. The following classification of North American Hadrosauridae, with the exception of *Claosaurus* and certain poorly defined forms, is proposed:

Class REPTILIA

Order ORNITHISCHIA Seeley
Suborder ORNITHOPODA Marsh

Family HADROSAURIDAE Cope
Subfamily HADROSAURINAE Lambe

Genera: *Thespesius, Hadrosaurus, Kritosaurus, Saurolophus, Gryposaurus, Prosaurolophus, Edmontosaurus, Anatosaurus, Brachylophosaurus.*

Subfamily LAMBEOSAURINAE Parks

Genera: *Trachodon, Hypacrosaurus, Corythosaurus, Cheneosaurus, Parasaurolophus, Lambeosaurus, Tetragonosaurus.*

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SOCIETY RECORDS AND ACTIVITIES

ANNUAL MEETING, PACIFIC COAST BRANCH OF THE PALEONTOLOGICAL SOCIETY

University of Washington, Seattle
March 26, 1954

At the annual meeting of the Pacific Coast Branch of the Paleontological Society in Seattle the following new slate of officers was elected:

Chairman: Orville L. Bandy, University of Southern California
Vice-Chairman: Harry E. Wheeler, University of Washington
Secretary: V. Standish Mallory, University of Washington
Councilman: W. H. Easton, University of Southern California

APPOINTMENT OF A CONSTITUTIONAL COMMITTEE

President Harry S. Ladd of the Paleontological Society announces the appointment of a Constitutional Committee comprising Messrs. Chalmer Cooper, chairman, John B. Reeside and Mackenzie Gordon, who will consider all proposals for changes in the Constitution or By-Laws proposed by members of the Society and report to the Council of the Society at the Los Angeles Council Meeting in November, 1954. Members who have suggestions to submit to this committee will please submit them to Chairman Cooper, U. S. Geological Survey, Washington 25, D. C., or to the Secretary of the Society.

KENNETH E. CASTER
Secretary

NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1 of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by the Council of the Society.

ACCORDI, BRUNO, Istituto di Geologia, Via Boldini 14, Ferra, Italy: Rees Leonardi.

BROOKS, JAMES ELWOOD, Dept. of Geology, Southern Methodist University, Dallas 5, Texas: C. C. Albritton, Jr., Grant Steele, L. L. Sloss.

ENGELBERTS, FREDERIK GERARD, c/o Compania Petrolera de Costa Rica Ltda. Apartado 3530, San Jose, Costa Rica: Walter Youngquist, Hans Thalmann.

FORTESCUE, JOHN ADRIAN CLAUDE, Geol. Dept. Univ. of British Columbia, Vancouver, B. C.: M. Y. Williams, V. J. Okulitch, A. S. Thomlinson.

ERBEN, HEINRICH KARL, Instituto de Geologia, 6a. del Cipres 176, Mexico, D. F.: Otto H. Schindewolf, J. B. Reeside, G. Arthur Cooper.

FREBOLD, FRIDTJOF, 537 Percy Street, Ottawa, Ontario: V. J. Okulitch, M. Y. Williams, A. S. Thomlinson.

GILBERT, RAY C., Austinville, Virginia: Byron N. Cooper, Wayne E. Moore.

HATCHER, ROY ALVIN, JR., 802 Richmond, Columbia, Missouri: A. G. Unklesbay, R. E. Peck.

HOLLISTER, SOLOMON CADY, College of Engineering, Cornell University, Ithaca, New York: K. E. Caster, K. V. W. Palmer.

IMBRIE, JOHN, Dept. Geology, Columbia Univ., New York 27: Marshall Kay, Roger L. Batten, Norman D. Newell.

MARIANOS, ANDREW W., 355 E. 2nd St., Chico, California: Grover E. Murray, H. V. Howe.

RAU, JON LLEWELLYN, 1116 Chestnut St., Grand Forks, North Dakota: F. D. Holland, Jr., Jesse B. Pogue, II, K. E. Caster.

SASTRY, M. V. A., Geological Survey of India, 27 Chowringhee, Calcutta, India: J. Wyatt Durham, Joseph H. Peck.

SAUNDERS, JOHN BAVERSTOCK, Trinidad Leaseholds Ltd., Pointe-A-Pierre, Trinidad, B. W.I.: Hans M. Bolli, Hans Thalmann.

SMYSOR, BETTIE LYONS, Dept. Geology and Geography, Univ. of Cincinnati, Cincinnati 21, Ohio: F. D. Holland, Jr., Jesse B. Pogue, II, K. E. Caster.

SPEED, CARLETON D., JR., 1315 Second National Bank Building, Houston, Texas: K. E. Caster, F. D. Holland, Jr.

WAITE, R. HAROLD, Dept. of Paleontology, Univ. of Calif., Berkeley, Calif.: J. Wyatt Durham, Robert M. Kleinpell.

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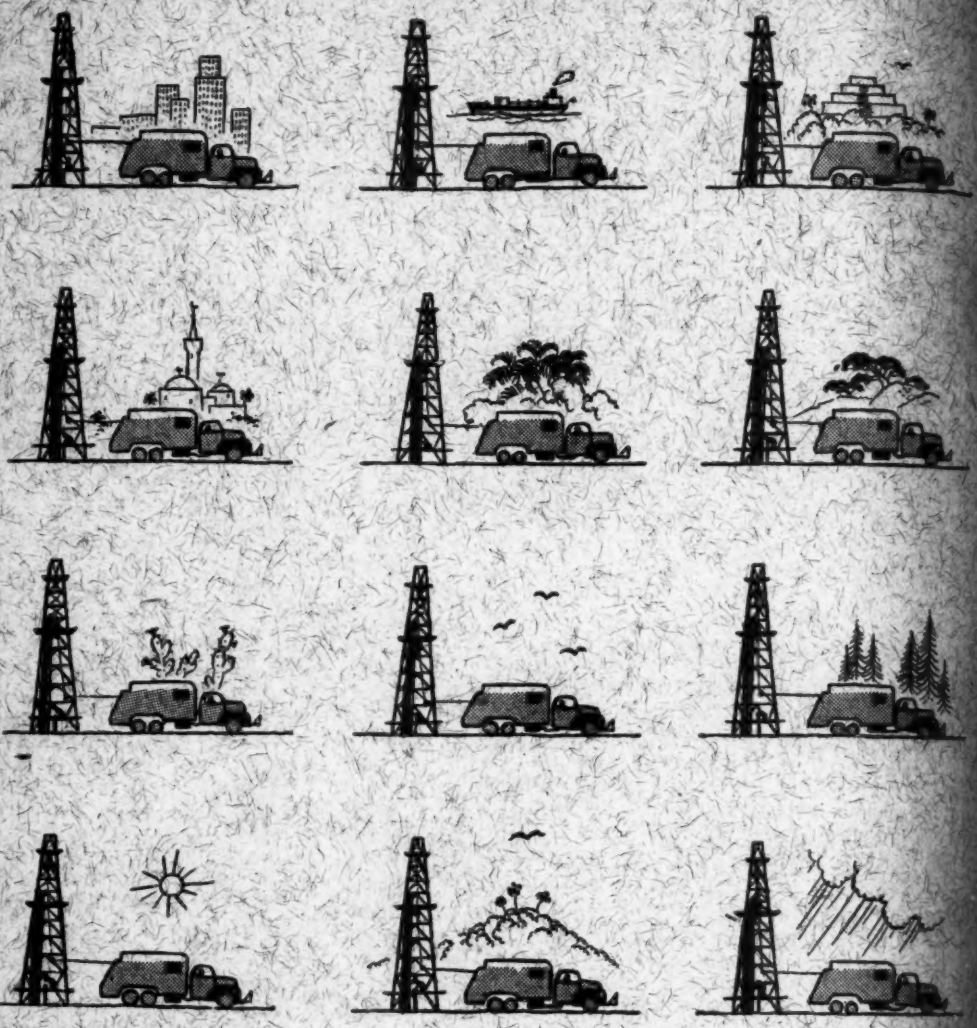

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